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ELAINE RIOS DA SILVA

INFLUÊNCIA DE PREDITORES ESPACIAIS E FATORES ANTRÓPICOS SOBRE MAMÍFEROS E AS CONSEQUÊNCIAS PARA REMOÇÃO DE SEMENTES EM REMANESCENTES DE MATA ATLÂNTICA

ILHÉUS – BAHIA

2021

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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.

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obrigada por esse amor incondicional.

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RESUMO

A biodiversidade vem sendo ameaçada a nível global pelas atividades antrópicas, incluindo mudanças no uso da terra principalmente para produção de comodities. Em florestas tropicais, essas modificações têm sido mais intensas, ocasionando impactos na diversidade e persistência de espécies, assim como na provisão de serviços ecossistêmicos. Nesse sentindo, nós investigamos como mudanças no uso da terra afetam os mamíferos florestais, grupo que desempenha papéis ecológicos fundamentais para o funcionamento dos ecossistemas, incluindo a dispersão de sementes. Especificamente, nós investigamos como mudanças na composição e configuração da paisagem, fatores antrópicos e características da história de vida das espécies, explicam padrões de riqueza e ocorrência dos mamíferos de médio e grande porte em remanescentes florestais de Mata Atlântica. Também avaliamos como essas alterações na abundância de mamíferos influenciam a remoção de sementes em remanescentes florestais localizados no sul da Bahia. Para isso, esta tese está dividida em três capítulos. Os dois primeiros consistem em uma revisão de literatura sobre estudos que realizaram amostragem de mamíferos ao longo da Mata Atlântica. No capítulo I, nós testamos a Hipótese da Quantidade de Habitat (HQH) e os efeitos da fragmentação *per se* sobre a riqueza de mamíferos, incluindo a assembleia total, espécies dependentes de floresta, generalistas de habitat e riqueza de guildas tróficas. Os resultados apoiam a HQH e apontam que os efeitos da fragmentação *per se* foram importantes apenas para explicar a riqueza de herbívoros. No capítulo II, nós avaliamos a influência de preditores espaciais, distúrbios antrópicos e dos atributos da história de vida das espécies na ocorrência de mamíferos terrestres, incluindo espécies dependentes de florestas caçadas e não caçadas e espécies generalistas. Encontramos que o padrão geral de ocorrência é determinado pelo tamanho do fragmento florestal, distúrbios antrópicos e massa corporal das espécies. Para as espécies florestais caçadas, a ocorrência foi determinada principalmente pela configuração da paisagem e distúrbios antrópicos, já a incidência das espécies florestais não caçadas, foi determinada especialmente pelo tamanho do fragmento florestal. Por outro lado, a ocorrência de generalistas foi explicada principalmente pela configuração da paisagem e distúrbios antrópicos. No capítulo III, nós avaliamos os efeitos diretos e indiretos de preditores espaciais, distúrbios antrópicos e abundância de mamíferos dispersores sobre o destino das sementes de biriba (*Eschweilera ovata*) em 18 fragmentos florestais situados no sul da Bahia. Em cada fragmento amostrado, nós usamos armadilhas fotográficas para amostragem dos potenciais mamíferos dispersores e realizamos um experimento com carretéis para avaliar o destino final das sementes. Descobrimos um efeito direto da cobertura florestal sobre a porcentagem de sementes removidas e um efeito da densidade humana sobre a abundância de mamíferos. Com base nos resultados encontrados nesta tese, nós demostramos a importância de manter uma elevada quantidade de floresta na paisagem e de considerar os efeitos da configuração da paisagem e dos distúrbios antrópicos para garantir alta riqueza, abundância e ocorrência de mamíferos. Nós também revelamos que a cobertura florestal afeta a remoção de sementes de *E. ovata* e que os mecanismos que explicam a dispersão dessas sementes podem ser mais complexos do que o previsto.

Palavras-chave: floresta tropical, distúrbios antropogênicos, espécies dependentes de florestas; espécies generalistas, guildas tróficas, dispersão de sementes.

INFLUENCE OF SPATIAL PREDICTORS AND ANTHROPIC FACTORS ON MAMMALS AND THE CONSEQUENCES FOR SEED REMOVAL IN ATLANTIC FOREST REMNANTS

ABSTRACT

Biodiversity has been threatened globally by human activities, including land use changes mainly for commodities production. In tropical forests, these changes have been more intense, leading to impacts on species diversity and persistence, as well as on the provision of ecosystem services. Here we investigate how land use changes affect forest mammals, a group that plays key ecological roles in ecosystem functioning, including seed dispersal. Specifically, we investigate how changes in landscape composition and configuration, anthropogenic factors and species' life history traits, explain the patterns of richness and occurrence of medium and large-sized mammals in forest remnants of the Atlantic Forest. We also evaluated how changes in mammal abundance influence seed removal in remnants located in southern Bahia. For this, the thesis is divided into three chapters. The first two consist of a literature review on studies that sampled mammals along the Atlantic Forest. In Chapter I, we tested the Habitat Amount Hypothesis (HAH) and the effects of fragmentation *per se* on mammal richness, including total assemblage, forest-dependent species, habitat generalists, and trophic guild richness. The results support the HAH and point out that the effects of fragmentation *per se* were only important to explain the richness of herbivores. In chapter II, we assessed the influence of spatial predictors, anthropogenic disturbances, and species life history attributes on the occurrence of terrestrial mammals, including hunted and non-hunted forest-dependent species and generalist species. We found that the general occurrence pattern is determined by patch size, anthropogenic disturbance and body mass. For hunted forest-dependent species, the occurrence was mainly determined by landscape configuration and anthropogenic disturbances, while the incidence of non-hunted forest-dependent species was mainly determined by patch size. The occurrence of generalist species was mainly predicted by landscape configuration and anthropogenic disturbances. In chapter III, we evaluated the direct and indirect effects of spatial predictors, anthropogenic disturbances and the abundance of mammal seed dispersers on seed fate of biriba (*Eschweilera ovata*) in 18 forest fragments located in southern Bahia. On each sampled fragment, we deployed camera traps to sample potential mammal seed dispersers, and performed a spool and line experiment to assess the final fate of the seeds. We found a direct effect of forest cover on the percentage of seeds removed and an effect of human density on mammal abundance. Based on the results found in this thesis, we demonstrate the importance of maintaining high amounts of habitat in the landscape and of considering the effects of landscape configuration and anthropogenic disturbances to ensure high richness, abundance and occurrence of mammals in the studied landscapes. We also highlight forest cover affects seed removal of *E. ovata*, however the mechanisms that explain the seed dispersal are more complex than previously thought.

Keywords: tropical forest, anthropogenic disturbances, forest dependent species, generalist species, trophic guilds, seed dispersal.

INTRODUÇÃO GERAL

As florestas estão entre os ecossistemas terrestres mais ameaçados mundialmente, devido à conversão de ambientes florestais em diferentes usos da terra, principalmente, em áreas para produção de comodities (CURTIS *et al*. 2018). De fato, 83% das terras destinadas para a agricultura na região tropical vieram à custa de florestas primárias e florestas perturbadas (GIBBS *et al*. 2010). Embora o papel das florestas primárias para conservação da biodiversidade seja insubstituível (GIBSON *et al*. 2011), essas mudanças no uso da terra geram paisagens modificadas pelo homem (PMHs), e entender como os organismos respondem a essas mudanças, é de fundamental importância para o desenvolvimento de estratégias para a conservação da biodiversidade e manejo dessas paisagens (Figura 1).


Fernando C. Bonfim

Figura 1: Fragmento florestal circundado por plantações de eucalipto e pasto localizado em uma paisagem antropizada de Mata Atlântica na região sul da Bahia, Brasil.

As PMHs podem apresentar diferenças tanto na composição de seus habitats (ou seja, nos tipos e quantidades de habitats disponíveis), quanto na configuração (ou seja, diferenças no arranjo espacial) (DUNNING *et al*. 1992). Inquestionavelmente, uma das primeiras consequências das mudanças no uso da terra é a perda de habitat, que tem impactos consistentes sobre a diversidade de espécies. Por exemplo, um declínio na riqueza e abundância de plantas arbóreas e lenhosas (ROCHA-SANTOS *et al*. 2017; BENCHIMOL *et al*. 2017), morcegos (MUYLAERT *et al*. 2016) e aves de sub-bosque (MARTENSEN *et al*. 2012) foi detectado em remanescentes florestais inseridos em paisagens com baixa cobertura florestal, uma medida frequentemente usada como *proxy* da quantidade de habitat para espécies florestais. Além da perda na quantidade de habitat, alterações na configuração da paisagem também podem ser observadas em PMHs, incluindo um aumento no número de fragmentos, uma diminuição no tamanho desses fragmentos e um aumento no isolamento entre eles, isto é, o processo de fragmentação (FAHRIG 2003). As informações sobre a importância e os impactos relativos à perda e fragmentação do habitat ainda estão sendo avaliados e intensamente debatidos (FAHRIG 2017; FAHRIG *et al*. 2019; FLETCHER *et al*. 2018; SAURA 2020). Destrinchar esses efeitos não é trivial, mas é fundamental que ocorra, uma vez que essas informações subsidiam políticas ambientais influenciando na gestão e uso das PMHs.

Além das mudanças na composição e configuração, outros atributos espaciais como a expansão da infraestrutura (ex: estradas) e presença humana também podem afetar a biodiversidade em fragmentos florestais. De fato, existe um crescente conjunto de evidências indicando que tanto as estradas quanto a presença humana estão relacionadas com as ameaças e extinções locais da biodiversidade (MCKINNEY 2001; BENÍTEZ-LÓPEZ *et al*. 2010; ESPINOSA *et al*. 2014). As estradas, por exemplo, podem criar efeitos de borda, funcionar como barreiras para o movimento e causar mortalidade da fauna por colisão, além de facilitar invasões humanas, o que pode causar sobre-exploração dos recursos naturais (FORMAN & ALEXANDER 1998; LAURANCE *et al*. 2009; PINTO *et al*. 2020). Esses impactos podem ser ainda mais intensos em florestas tropicais, pois elas abrigam altos níveis de biodiversidade e geralmente situam-se em nações em desenvolvimento econômico (MYERS *et al*. 2000), que muitas vezes estão experimentando um rápido crescimento populacional e um aumento na exploração de recursos naturais (OYETUNJI et al. 2020).

Um bioma singular para entender como as alterações antrópicas podem afetar a biodiversidade é a Mata Atlântica. Considerada a segunda maior floresta da América do Sul, a Mata Atlântica se destaca por seus altos níveis de endemismo e degradação do habitat (MYERS *et al*. 2000). Abrigando cerca de 72% da população humana brasileira e restando apenas 28% da sua cobertura vegetal original, é atualmente uma das florestas mais ameaçadas e importantes para conservação da biodiversidade (REZENDE *et al*. 2018; SOS MATA ATLÂNTICA & INPE 2020). Especialmente a Mata Atlântica da região sul do Estado da Bahia (Figura 2), considerada um dos centros de endemismo e *hotpoints* de biodiversidade (SILVA & CASTELETI 2003; MARTINI *et al.* 2007), experimenta um longo e intenso processo de ocupação humana e mudanças no uso da terra (FARIA *et al*. 2021). Nos últimos anos o Estado esteve entre os que mais desmataram (SOS Mata Atlântica & INPE 2017; 2018; 2019) e, atualmente, lidera o ranking de desmatamento no bioma (SOS Mata Atlântica & INPE 2020). Além disso, os remanescentes florestais se encontram sob fortes pressões humanas, incluindo a extração seletiva de madeira e outros produtos florestais e a caça de animais silvestres (Figura 3) (CASTILHO *et al*. 2017). Lamentavelmente, é provável que essas ameaças se intensifiquem com o enfraquecimento e desmonte das leis ambientais pelo atual governo brasileiro (BARBOSA *et al*. 2021).

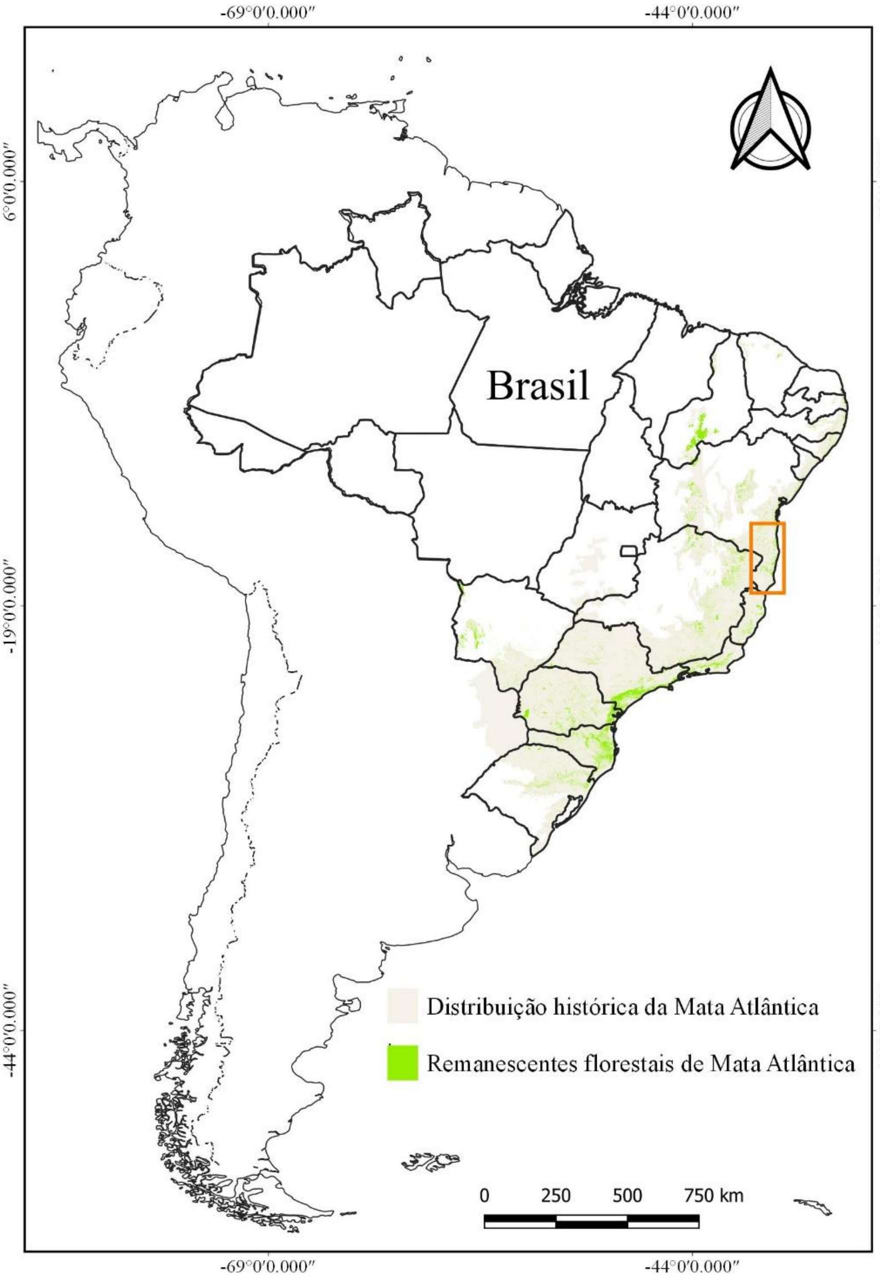

Figura 2. Distribuição histórica e atual da Mata Atlântica com destaque para a região sul do Estado da Bahia, Brasil.

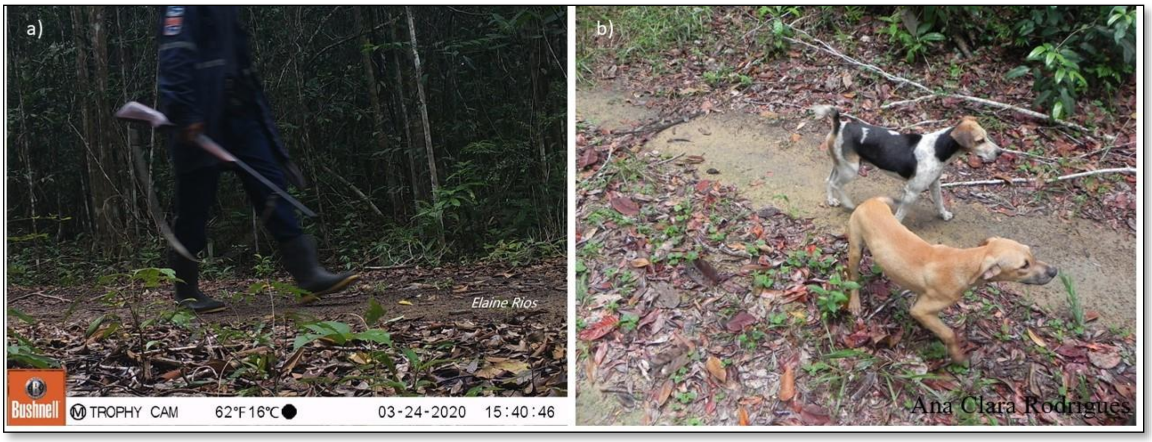

Figura 3. Vestígios de atividades de caça em fragmentos florestais de Mata Atlântica na região sul da Bahia, Brasil. a) caçador registrado por uma armadilha fotográfica instalada neste estudo e b) cachorros domésticos encontrados durante atividades de campo.

Apesar das mudanças na paisagem e distúrbios crônicos causarem um declínio abrupto na diversidade de espécies em paisagens antropizadas (NEWBOLD *et al*. 2015; 2016), as espécies animais podem apresentar respostas distintas a essas perturbações, influenciado os seus padrões de ocorrência. Particularmente, os efeitos combinados das características biológicas intrínsecas das espécies e o nível de perturbação no habitat determinam a ocorrência de cada espécie. Características como o grande tamanho corporal, baixas taxas reprodutivas, dieta mais restritiva e grandes áreas de vida tornam algumas espécies mais vulneráveis e, quando essas características são combinadas com intensas perturbações no habitat, o risco de extinção pode aumentar acentuadamente (ROBINSON & REDFORD 1986; CARDILLO *et al*. 2005; 2008). Por exemplo, o tamanho do fragmento combinado com o nível de pressão de caça, tamanho da área de vida e status trófico foram os principais preditores da persistência de espécies de primatas em fragmentos florestais na região neotropical (BENCHIMOL & PERES 2014). Assim, os efeitos aditivos da área do habitat, contexto da paisagem e as características da história de vida podem ajudar a prever a persistência das espécies animais em PMHs

(MICHALSKI & PERES 2005; THORNTON *et al*. 2011; BENCHIMOL & PERES 2015).

De maneira similar, espécies que possuem especificidades de habitat distintas também variam em suas respostas às mudanças na paisagem. Por exemplo, espécies que apresentam alto grau de especialização de habitat são mais sensíveis às mudanças em seu habitat (ex: especialistas de habitat), e tendem a ser afetadas negativamente. Esse padrão foi observado para alguns grupos como aves especialistas em floresta (MORANTE-FILHO *et al*. 2015) e espécies arbóreas (ROCHA-SANTOS *et al*. 2017), os quais declinaram em paisagens mais desmatadas de Mata Atlântica, e para assembleias de pequenos mamíferos dependentes de floresta que foram afetados negativamente pela perda de habitat na Amazônia (PALMEIRIM *et al*. 2020). De maneira contrária, as espécies generalistas de habitat que possuem forte tolerância a perturbações como o desmatamento podem ser adaptar e persistir em PMHs (PARDINI *et al*. 2009; MORANTE-FILHO *et al*. 2015).

Dentre os vertebrados florestais, os mamíferos compreendem um excelente grupo para avaliar quais fatores influenciam a persistência ou causam o declínio da riqueza de espécies em PMHs. De fato, os mamíferos constituem um grupo diverso, com suas espécies apresentando amplas variações no tamanho corporal, dieta, uso do habitat e tolerância aos distúrbios ambientais (EMMONS & FEER 1997; PAGLIA *et al*. 2012; ver Figura 4). Desempenham ainda funções críticas para o funcionamento dos ecossistemas como controle *top-down* (TERBORGH 1992; TERBORGH *et al*. 2001), herbivoria (VALVERDE et al. 2020), são agentes essenciais para dispersão e predação de sementes (WRIGHT & DUBER 2001; MITTELMAN et al. 2021; BUENO *et al*. 2013), e ainda compreendem uma fauna carismática com muitas espécies sendo usadas como símbolos em projetos de conservação. Por outro lado, mamíferos experimentam declínios acentuados de suas populações e extinções locais direcionadas principalmente por atividades humanas (BOGONI *et al*. 2020; PEREIRA et al. 2021), incluindo a perda de habitat (CANALE *et al*. 2012) e caça excessiva (RIPPLE *et al*. 2016; BENÍTEZ-LÓPEZ *et al*. 2017). Atualmente, cerca de 26% das espécies de mamíferos encontra-se em alguma categoria de ameaça, com um total de 587 espécies ameaçadas apenas no Brasil (IUCN 2021).

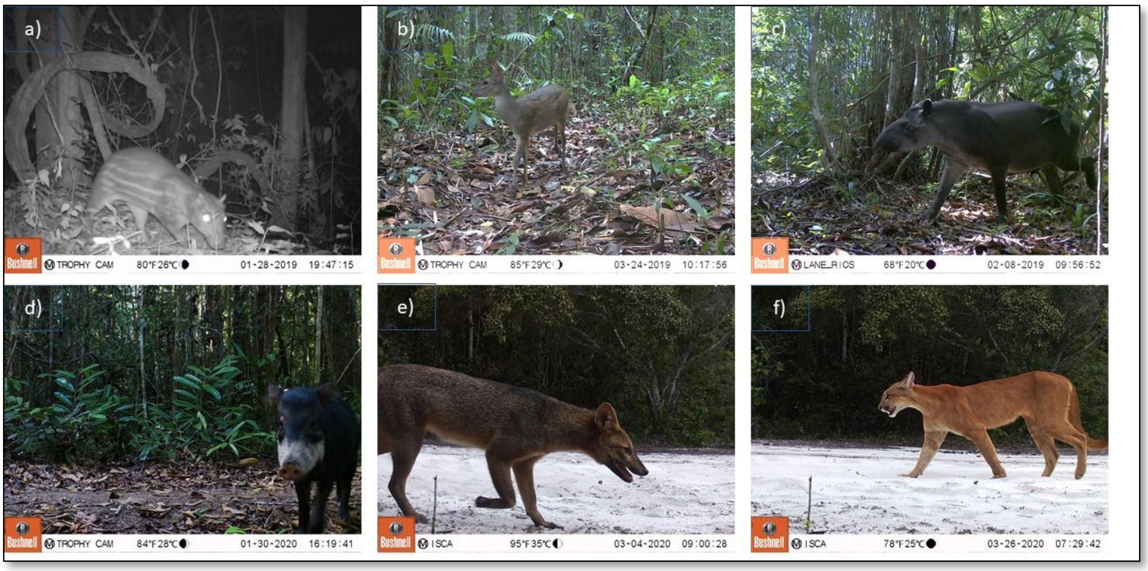

Figura 4: Espécies de mamíferos registradas com armadilhas fotográficas em fragmentos florestais de Mata Atlântica na região sul da Bahia, Brasil. a) paca (*Cuniculus paca*), b) veado (*Mazama* sp.), c) anta (*Tapirus terrestris*), d) queixada (*Tayassu pecari*), e) cachorro-do-mato (*Cerdocyon thous*) e f) onça parda (*Puma concolor*).

A defaunação, ou seja, a extinção de espécies da fauna, populações ou declínio na abundância de indivíduos dentro das populações (YOUNG *et al*. 2016), tem impactos profundos na estrutura e funcionamento dos ecossistemas tropicais. De forma geral, a defaunação ocorre de forma seletiva, onde espécies com tamanhos corporais maiores são as mais afetadas, principalmente porque são as espécies preferencialmente caçadas e necessitam de grandes áreas de habitat para persistirem (DIRZO *et al*. 2014). Como consequência, os mamíferos estão entre os grupos mais ameaçados e isso tem várias implicações para o funcionamento das florestas. Por exemplo, dentre as funções críticas desempenhadas por mamíferos, a dispersão de sementes é importante para a persistência e distribuição de diversas espécies de plantas (MITTELMAN et al. 2021; TERBORGH *et al*. 2008). Particularmente, grandes mamíferos possuem um papel de destaque nesse processo devido a sua capacidade em dispersar um grande número de sementes e transportá-las por longas distâncias (BUENO et al. 2013), especialmente aquelas sementes de maior tamanho que outras espécies não conseguem dispersar (FRAGOSO 1997; FRAGOSO *et al*. 2003). Por exemplo, a espécie *Joannesia princeps*, uma árvore tropical que possui sementes grandes, tem uma alta dependência das cutias (*Dasyprocta leporina*) para dispersarem suas sementes (MITTELMAN *et al*. 2021). No entanto, a perda direcional de mamíferos pode afetar essas espécies animais que são as únicas capazes de realizar essa função, podendo levar a falhas no processo de dispersão dessas sementes grandes (TERBORGH et al. 2008; POULSEN *et al*. 2013; PERES *et al*. 2016), com sérias consequências para outros serviços ecossistêmicos, incluindo o sequestro e armazenamento de carbono (BELLO *et al*. 2015).

Visando entender como atributos espaciais como, tamanho do fragmento florestal, composição e configuração da paisagem, assim como fatores antrópicos afetam a riqueza, abundância e ocorrência das espécies de mamíferos da Mata Atlântica brasileira e os processos ecológicos desempenhado por elas, esta tese foi estruturada em três capítulos. Os dois primeiros capítulos consistem em uma revisão sistemática de literatura sobre estudos que realizaram amostragem de mamíferos de médio e grande porte em fragmentos florestais ao longo de toda a Mata Atlântica. No capítulo I, nós avaliamos a hipótese da quantidade de habitat e os efeitos da fragmentação *per se* sobre a riqueza de mamíferos, incluindo além da riqueza total, a riqueza de espécies dependentes de floresta, espécies generalistas e riqueza de guildas tróficas (carnívoros, insetívoros, frugívoros, onívoros e herbívoros). No capítulo II, nós avaliamos como os diferentes atributos espaciais e as características da história de vida das espécies podem determinar o padrão geral de ocorrência de mamíferos terrestres, incluindo espécies dependentes de florestas caçadas, espécies dependentes de florestas não caçadas e espécies generalistas de habitat. No capítulo III, nós avaliamos os efeitos diretos e indiretos de preditores espaciais e a abundância de mamíferos (incluindo espécies dispersoras e predadoras de sementes) na remoção de sementes de biriba (*Eschweilera ovata*; Lecythidaceae) em 18 fragmentos florestais localizados em paisagens antropizadas contrastantes de Mata Atlântica na região sul da Bahia, Brasil.

CAPÍTULO I

TESTING THE HABITAT AMOUNT HYPOTHESIS AND FRAGMENTATION EFFECTS FOR MEDIUM- AND LARGE-SIZED MAMMALS IN A BIODIVERSITY HOTSPOT

(https://link.springer.com/article/10.1007/s10980-021-01231-9)

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Testing the habitat amount hypothesis and fragmentation effects for medium- and large-sized mammals in a biodiversity hotspot

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Abstract

Context Habitat loss is widely recognized as the main driver of biodiversity loss around the globe, yet the effects of habitat fragmentation on biodiversity have been extensively debated in recent years. *Objectives* We used a robust dataset of medium and large-sized mammals to test (a) the Habitat Amount Hypothesis, which postulates that species richness can be mainly predicted by the total amount of habitat surrounding the sampling site, and (b) the effects of habitat fragmentation per se, which may be expected to be weak or mainly positive on species richness.

Methods We compiled information on the occurrence of mammal species in 166 forest fragments across the Atlantic Forest. For each forest fragment, we extracted information on patch size, percentage of forest cover (a proxy for habitat amount), and edge density and number of fragments (fragmentation metrics). We related these metrics to mammalian richness considering separately for all species, forest-dependent species, disturbance-tolerant species, and different trophic guilds.

Results All richness measures strongly declined with decreasing forest cover, yet were unaffected by patch size, number of patches and edge density. The only exception occurred with herbivore richness, which was affected by number of patches. However, we found fragmentation per se effects only for herbivore richness.

Conclusions Our results show that mammal richness increased with habitat amount at the landscape, whereas habitat fragmentation per se had significant negative impacts on herbivores only. We therefore recommend maintaining highly forested landscapes and restoring severely deforested areas, being essential for ensuring high richness of mammals.

Keywords: Atlantic forest; Fragmentation per se; Habitat loss; Landscape composition; Landscape configuration; Trophic guilds

Introduction

The rapid loss of natural environments is currently considered the main threat to biodiversity worldwide (Newbold et al. 2015, 2016). In the tropics, large tracts of pristine forests are being replaced by agriculture, pastures and urban expansion areas transforming natural environments into a mosaic of forest patches (Gibbs et al. 2010; Curtis et al. 2018). Habitat loss and fragmentation are different processes, though generally associated, and both can result from anthropogenic land conversion (Fahrig 2003). Recognizing the independent effects of habitat loss and fragmentation on ecological responses is crucial for effective decision making, as species can respond differently to these processes and inappropriate decisions may compromise the efficiency of conservation measures (Lindenmayer and Fischer 2007; Mortelliti et al. 2010).

The Habitat Amount Hypothesis (HAH), proposed by Fahrig (2013), states that species richness should be predicted by the habitat amount in the landscape surrounding the sample site (Fahrig 2013). This hypothesis suggests that the two predictive variables of the Theory of Island Biogeography (MacArthur and Wilson 1967)—patch size and isolation—can be replaced by a single variable, the habitat amount in the landscape. Despite its relatively recent proposition, the HAH has been tested by several studies. For instance, a global synthesis of species density studies of eight taxonomic groups showed that richness was more strongly and positively related to habitat amount, whereas habitat fragmentation metrics unaffected patterns of species richness for the groups evaluated (Watling et al. 2020). Additionally, studies focused on birds (De Camargo et al. 2018), beetles (Seibold et al. 2017) and small mammals (Melo et al. 2017; Vieira et al. 2018) also supported the HAH. Yet some studies failed to support this hypothesis (see Haddad et al. 2016; Bueno and Peres 2019), suggesting that in some cases patch size and isolation might be more decisive than habitat amount.

In contrast to the robust evidence on the pervasive effects of habitat loss on biodiversity, there is no consensus on the effects of fragmentation per se (sensu Fahrig 2003, 2017: the breaking apart of habitat, independent of changes in habitat amount) on biological components. For instance, a recent review showed that when habitat amount is controlled, there are often no additional effects of landscape configuration (i.e. fragmentation) on species' ecological responses and that when fragmentation effects are detectable, they are mostly positive (Fahrig 2017). This publication ignited an intense debate among researchers (Fahrig 2017; Fletcher Jr et al. 2018; Fahrig et al. 2019) on whether the independent effects of habitat fragmentation per se are positive (Fahrig 2003, 2017) or negative (Reino et al. 2013; Rueda et al. 2013). Disentangling the effects of habitat loss and fragmentation is challenging but necessary for conservation decisions.

An interesting scenario to assess the independent effects of habitat amount and fragmentation per se is the Brazilian Atlantic Forest. This biome extends over 112 Mha distributed along the Brazilian coast; current estimates indicate that 28% of the original native cover remains, with 26% corresponding to forest areas (Rezende et al. 2018). Most of these forest fragments are very small (< 50 ha) and isolated (at an average distance of 1.5 km from one another; Ribeiro et al. 2009). In addition to deforestation, the Atlantic Forest is also highly threatened by poaching (Galetti et al. 2009) and human occupation, severely impacting local fauna (Bogoni et al. 2016). It also harbors one of the highest degrees of biodiversity and endemism for several plant and animal groups, being recognized as a global biodiversity hotspot (Myers et al. 2000). For instance, this biome is home to 321 mammal species, with 89 endemic ones (Graipel et al. 2017).

The importance of mammals for ecosystem structure and functioning is widely recognized (Galetti and Dirzo 2013) due to their key role in community structuring (Jorge et al. 2013), seed predation and dispersal, and their contribution to forest carbon stocks (Bello et al. 2015). Mammals are highly threatened mainly by changes in their habitat (Jorge et al. 2013) and hunting (Cullen Jr et al. 2000; Galetti et al. 2009). Thus, the intense history of deforestation and hunting that occurred in the Atlantic Forest led to pronounced current changes in species composition of mammal assemblages (Canale et al. 2012). Disturbance sensitive species are the first to disappear in highly disturbed areas, whereas alien and disturbance-tolerant species tend to become dominant in forest fragments (Jorge et al. 2013; Beca et al. 2017). Changes in community composition can also be detected, as functional groups tend to respond non-randomly to changes in their habitat. For example, species that require large home ranges to survive, such as carnivores, tend to be negatively affected by human disturbances, whereas omnivorous and insectivorous species are prone to exhibit great plasticity and be less impacted (Bogoni et al. 2016; Regolin et al. 2017).

Here, we gathered and analyzed a robust dataset on the occurrence of medium to large-bodied mammal species for a wide range of forest patches throughout the Atlantic forest to (a) test the habitat amount hypothesis and (b) evaluate the effects of forest fragmentation per se on this group. We evaluated species richness considering the complete assemblage, the forest-dependent and disturbance-tolerant species separately and the species within each trophic guild (i.e., carnivores, insectivores, frugivores, omnivores and herbivores) individually. Specifically, we expected that (a) richness patterns would be better explained by the amount of habitat than by patch size or by fragmentation per se metrics (i.e., edge density and number of patches; Watling et al. 2020) when considering the complete assemblage and investigated groups, and (b) the effects of fragmentation per se on species richness would be mainly positive (Fahrig et al. 2017).

Methods

Data base

We gathered information on the occurrence of medium- and large-sized mammal species (all terrestrial and arboreal wildlife species larger than 1 kg; see Paglia et al. 2012) within forest fragments (defined as forest patches > 1 ha) from published studies conducted in the Atlantic Forest. In July 2019, we first searched studies using the Scopus and Google Scholar databases, specifying the terms "Atlantic Forest" AND "medium-sized (bodied) mammal" AND/OR "large-sized (bodied) mammal". We further used the same terms in Google Scholar, but only evaluated the first 200 results. We finally included records from the “ATLANTIC-CAMTRAPS” datapaper (Lima et al. 2017). We included studies if they provided (a) the geographic coordinates of the forest fragment(s), (b) the complete list of species recorded per forest fragment(s), and (c) if the data were obtained using camera traps, linear transects, or sign surveys (i.e. feces, playbacks, hair, and footprints), excluding secondary data and interviews. We did not include island patches and reviews. Whenever different studies sampled the same forest fragments, we combined the information and considered them as a single study, resulting in 67 studies carried out in 166 forest fragments (see Appendix S1 in Supporting Information). All forest fragments belonged to either protected or private areas, and were vastly distributed throughout the Brazilian Atlantic Forest, in areas of dense, mixed or semideciduous ombrophilous forest (Fig. 1). The size of forest fragments varied from 1.030 ha to more than 41,700 ha (mean = 2591.19 ha, SD = 6,974.74 ha), and the surrounding land uses consisted mainly of agriculture, pasture, and urban areas.

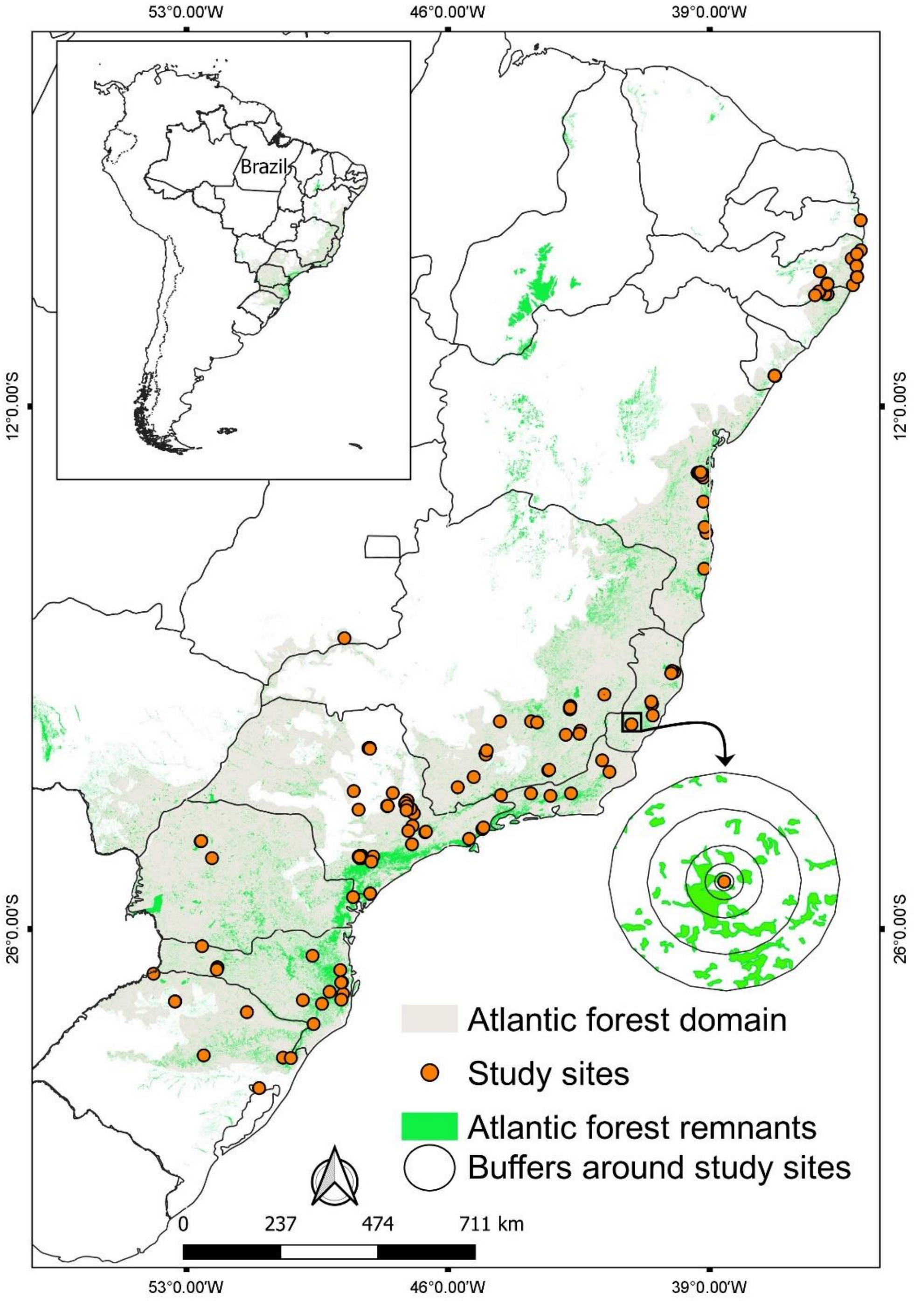

Fig. 1 Geographic distribution of the 166 forest fragments with records on the occurrence of medium and large-sized mammals along the Atlantic Forest, Brazil. The highlighted circular area is an example of landscapes of 0.5, 1, 2, 4 and 6 km of radius around a sampling site where the variables were calculated

We obtained total species richness for each forest fragment by summing all occurrences of the target mammalian group. However, we only considered forest-dwelling species into our database, excluding those species that use forest environments but have preferences for other types of habitats. For example, we excluded the maned wolf (*Chrysocyon brachyurus*) and the giant anteater (*Myrmecophaga tridactyla*), as these species most often use open areas like savannas and grasslands. We also excluded species like the Neotropical otter (*Lontra longicaudis*) and capybara (*Hidrochoerus hydrochaeris*), which is strongly associated with aquatic environments. Finally, we excluded exotic and opportunistic species such as feral pigs (*Sus scrofa feral*) and domestic dogs (*Canis lupus familiaris*) and difficult-to-detect species, such as the maned three-toed sloth (*Bradypus torquatus*) and the brown-toed sloth (*B. variegatus*), due to the high probability of false negatives. We thus included 55 species in our study (Table S1).

Although all species included in our database were forest-dwelling species, we further classified them in two categories, according to their tolerance to disturbances based on the literature (see Emmons and Feer 1997; Souza et al. 2019; IUCN 2019): (i) forest-dependent species, which are those found in non-disturbed forests and most frequently in forest interior, and (ii) disturbance-tolerant species, which comprise those more tolerant to anthropogenic disturbances, occurring frequently in disturbed forests or forest edges. In addition, we classified species into trophic guilds: carnivores, insectivores, frugivores, omnivores and herbivores, following Magioli et al. (2015).

Habitat amount and fragmentation metrics

We extracted patch size (in hectares) from the studies or, when not available, calculated it using Google Earth Pro. We then obtained landscape metrics using the maps from

MapBiomas Project– Collection [4, 2019] derived from 30-m resolution Landsat imagery, downloaded from the Brazilian Annual Land Use and Land Cover Mapping Project (available at < https://mapbiomas.org/ >). For each forest fragment, we used the map corresponding to the last year in which data collection was performed in each study.

Forest cover was calculated as the proportion of native forest (excluding agroforestry), considering buffers of 0.5, 1, 2, 4 and 6 km radius around each sampling point provided by the study. These scales were selected based on the literature showing that medium and large-sized mammals best respond to landscape characteristics at large scales and according to the species' dispersal ability (Lyra-Jorge et al. 2010; Beca et al. 2017; Regolin et al. 2017). To test the fragmentation per se effects, we obtained two fragmentation metrics: the edge density, calculated as the total perimeter of all forest fragments divided by the size of the landscape, and the number of forest patches within each landscape. Analyses were performed in R 3.5.2 (R Core Team 2018) and QGIS® software.

Data analysis

We firstly evaluated the scale of effect—the spatial extent at which a certain landscape characteristic has the strongest impact on the dependent variable (Martin and Fahrig 2012; Fahrigh 2013) for each landscape variable. For this, we adjusted Generalized Linear Models (GLM) using the 'Multifit' function (Huais 2018), which automates the selection process at various scales and relates the response variable to each explanatory variable. We then used Akaike's Information Criterion (AIC) to classify the models, selecting the 'best' scale as the one showing the lowest AIC. The scale of effects varied between 0. 5, 1, 2 and 4 km, for different metrics (Table S2).

Forest fragments were considered spatially nested within several regions. Using QGIS software, we distinguished regions by combining groups of forest fragments according to the presence of large geographical barriers such as (1) large rivers, belonging to the main hydrographic basins that occur in the Atlantic Forest, (2) mountainous areas, using relief information, and (3) fragments belonging to extensive areas of forest, using Google Earth images. We extracted this information from the Brazilian Institute of Geography and Statistics (IBGE 2017) and Google Earth Pro tools. We transformed patch size values into logarithm (Log10) to homogenize the spread of the data. Due to differences in measurement units between the explanatory variables, we standardized their values by subtracting the mean and dividing by the standard deviation. Although sampling effort varied among surveyed forest fragments, we were unable to obtain this information for most of fragments included in our database. Additionally, different sampling techniques were used among studies, which also implies in different units of sampling effort. Therefore, we were unable to account for sampling effort in the GLMs. We used Variance Inflation Factors (VIF) (Zuur et al. 2009) to verify the collinearity between the explanatory variables. The VIF was always below 3, and, considering the ecological importance of all variables, we kept all of them in further analyses (Dormann et al. 2013) (Table S3).

To test the HAH on mammal richness, we first adjusted GLMs, with negative binomial distribution, containing all explanatory variables (i.e., patch size, forest cover, edge density and number of patches), for each response variable (richness of all species, forest-dependent and disturbance-tolerant species, and different trophic guilds), with no interactions. Subsequently, we verified the residual spatial autocorrelation using Moran's I and semivariograms. As the residuals were spatially autocorrelated, we adjusted Generalized Linear Mixed Models (GLMMs), which are appropriate to control for spatial non-independence (Zuur et al. 2009). Thus, we incorporated the terms ’region’ and ’data type’ into the models as random factors. The variable ’data type’ corresponds to the different data collection methods (camera trap, linear transect or sign surveys). For ‘data type’, we included all methods cited in each study analyzed. We re-evaluated spatial autocorrelation using the same procedure as above, and no further corrections were necessary.

We performed Multimodel Inference (Burnham and Anderson 2002) using the function ‘dredge’, which compares all subsets of models with all possible combinations of explanatory variables plus a null model, resulting in a total of 16 models being compared for each response variable. Afterwards, we used the function ’importance’ to calculate the relative importance of each explanatory variable (Burnham and Anderson 2002). This function sums the Akaike weights of models including each explanatory variable; variables with larger summed weights are more important than variables with smaller weights (Burnham and Anderson 2002). Finally, we evaluated the significance ($p < 0.05$) and direction (positive or negative) of the effect of each explanatory variable, using the model averaging approach, which calculates the average of the coefficients of all models weighted by the Akaike weights (Burnham and Anderson 2002).

To test the fragmentation per se effects on mammal richness, we adjusted GLMMs (with negative binomial distribution and the same random factors as above) containing habitat amount as the only explanatory variable. We then extracted the model Pearson residuals (calculated as the observed minus the expected value, divided by the square root of the variance – Zuur et al. 2009) in order to control the effects of habitat amount on the response variables. Finally, we used linear regressions to relate the residuals to fragmentation metrics (edge density and number of patches). With this, we aimed to assess whether the fragmentation metrics can explain variation that was not explained by habitat amount. We assessed whether there was an effect by analyzing the p-value; when it was significant ($p \leq 0.05$) we also checked whether the relation was positive or negative. All analyses were carried out in R 3.5.2 (R Core Team 2018), using the lme4 (Bates et al. 2015), MASS (Venables and Ripley 2002) and MuMIn (Barton 2020) packages.

Results

From the total of 55 mammal species recorded at least once in all forest fragments included in our final databse, 33 were classified as forest-dependent species while 22 comprise disturbance-tolerant species. They belong to nine orders: Primates, Rodentia, Cingulata, Lagomorpha, Cetartiodactyla, Perissodactyla, Pilosa, Carnivora and Didelphimorphia. The most common species were the nine-banded armadillo (*Dasypus novemcinctus*) (62%), followed by the South-American coati (*Nasua nasua*) (56%), the crab-eating fox (*Cerdocyon thous*) (49%) and the crab-eating raccoon (*Procyon cancrivorus*) (44%), whereas the agouti (*Dasyprocta iacki*) and the southern long-nosed armadillo (*Dasypus hybridus*) had a single record each.

Forest cover had positive effects and was the most important variable explaining richness patterns of medium and large-bodied mammals, independent of the disturbance tolerance or the trophic guild evaluated (Fig. 2). The exception was the insectivores, in which edge density was the most important variable. For omnivores and herbivores, respectively, edge density and number of patches were also important. The second most important variable was the number of patches, partially explaining richness patterns of the overall community, forest-dependent species, carnivores, frugivores and herbivores. However, only herbivores richness was significantly affected by the number of patches. The patch size and edge density did not significantly explain species richness of any group (Fig. 2; Tables S4; S5).

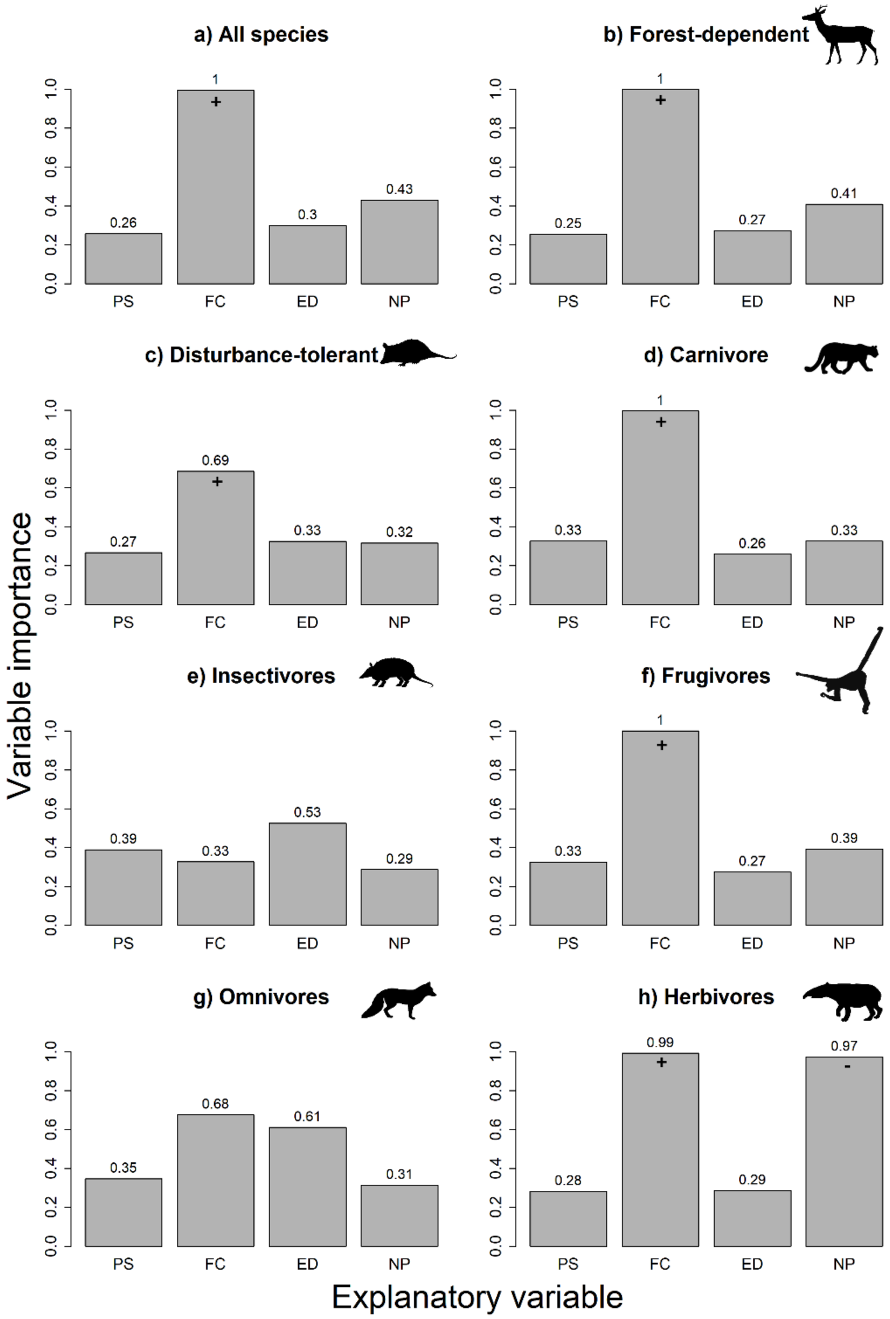

Fig. 2 Relative importance of each spatial variables: (PS) patch size, (FC) forest cover, (ED) edge density and (NP) number of patches for mammal species richness considering: **a** all species, **b** forest-dependent, **c** disturbance-tolerant, **d** carnivores, **e** insectivores, **f** frugivores, **g** omnivores and **h** herbivores. Values correspond to the sum of Akaike weights of the models containing each explanatory variable. The (+) and (−) corresponds to the variables that had a significant positive and negative effect, respectively

Regarding the fragmentation per se effects, our results showed no relationship between the residuals of species richness and the fragmentation metrics except for herbivores that were negatively influenced by the number of patches. This shows that, in general, habitat fragmentation per se had no effect on mammal richness after accounting for the effects of habitat amount (Fig. 3).

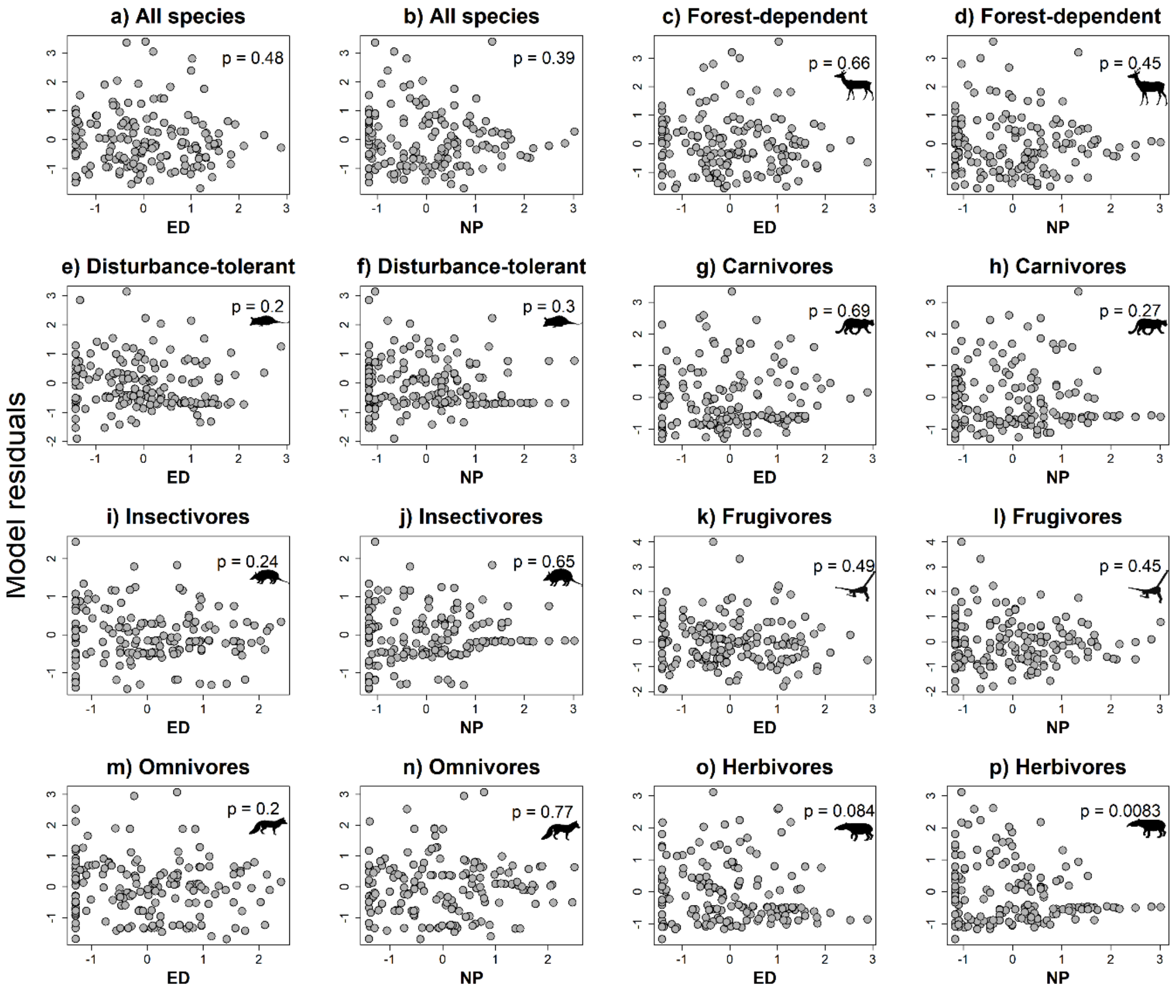

Fig. 3 Relationship between forest cover model residuals and fragmentation variables (ED—edge density and NP—number of patches), for medium and large-sized mammals of the Atlantic Forest in relation to the richness of: **a** all species, **b** forest-dependent, **c** disturbance-tolerant, **d** carnivores, **e** insectivores, **f** frugivores, **g** omnivores and **h** herbivores

Discussion

Our results show that habitat amount is the most important predictor explaining the richness of medium and large-sized mammals inhabiting forest patches in the Brazilian Atlantic Forest. We also found that fragmentation per se had no effects on mammal richness, except for herbivores. The combination of these results reinforces the importance of habitat amount over fragmentation to explain species richness, independent of the functional differences between the groups analyzed. Our study thus adds more evidence to the importance of forest cover to safeguard biodiversity, with direct and simple conservation strategies focused on mammals – maximizing the habitat amount in the landscape.

Habitat amount hypothesis

Our results support the HAH, as forest cover, used as a proxy for habitat amount, was the most important predictor of mammal species richness. The same pattern has been observed for medium and large-sized mammals in the southern region of Brazil (Regolin et al. 2017) and small specialist mammals in the Brazilian Cerrado (Melo et al. 2017). Yet forest-dependent small mammals responded equally to habitat amount and isolation in another study (Vieira et al. 2018). In addition to mammals, other groups have also responded positively to increases in habitat amount, including saprophytic beetles (Seibold et al. 2017), moths (Merckx et al. 2019) and birds (Lindenmayer et al. 2020). Although sampling effort was not included in our data analyses given the absence of this information on most studies coupled with the inclusion of different sampling methodologies in our database, we still found a strong relationship between species richness and habitat amount. In fact, this reinforces the hypothetical consistency of the habitat amount effects, since other studies took into account the sampling intensity (De Camargo et al. 2018; Palmeirim et al. 2019).

Our results also showed that species exhibiting contrasting responses to environmental disturbances, such as forest-dependent and disturbance-tolerant species, responded similarly to the habitat amount in the landscape. In general, forest cover was also the most important variable explaining richness of all functional groups analyzed, especially the richness of carnivores, frugivores, omnivores and herbivores. These results reinforce the importance of highly forested landscapes to safeguard large-bodied mammal species, a unique ecological group but which had their ranges intensely reduced due to the loss and degradation of their habitats (Canale et al. 2012; Jorge et al. 2013). In fact, the disappearance of frugivore and herbivore species from forest fragments can have pervasive implications for forest functionality. For example, the extinction of the white-lipped peccary, a large-bodied herbivore that is also an important seed disperser and predator, had strong negative impacts on the composition of small mammal communities in southeastern Brazil (Galetti et al. 2015), while the disappearance of species such as tapir can compromise populations of species with large seeds and long-distance dispersal (Galetti et al. 2001).

Patch size did not affect medium and large-sized mammals in the Atlantic forest. This contrasts to other studies that have found that patch size is a key predictor of mammal richness (Benchimol and Peres 2015; Michalski and Peres 2007). Conversely, edge density was an important variable to explain richness patterns of insectivores, also being the second variable with the highest weight for omnivores, but without significant effects. Conversely, the number of patches was the second most important variable to explain species richness of most of the groups analyzed, having a significant negative effect only for herbivores. Although edge density did not have a significant effect, such negative relationships with edge density have been observed for the richness of carnivorous mammals in areas of Atlantic Forest and Savanna, in Brazil (Lyra-Jorge et al. 2010). This negative effect may be related to microclimate and forest structure changes due to edge effects (Murcia 1995; Harper et al. 2005). In addition, species responses to edge density can generally be related to how species exploit resources in the landscape and the availability of resources at the edges and in the matrix (Ries and Sisk 2004). For example, more habitat-generalist species with high dispersion capacity tend to benefit at the edges (Lyra-Jorge et al. 2010; Pfeifer et al. 2017). However, this has not been confirmed here, even for groups that have lower specific diets, such as insectivores and omnivores. Similarly, the negative effect of the number of patches on species richness, especially for herbivores, might be explained by the matrix surrounding the forest fragments analyzed here, which mainly consisted of agriculture and cattle pasture areas. As the matrix quality can influence the connectivity between habitat fragments in the landscape (Arroyo-Rodriguez et al. 2020), it is possible that croplands and pastures represent a less permeable matrix for these species, as these environments reduces connectivity between forest fragments (Watling et al. 2011). This negative relationship with edge density and number of fragments in the landscape may accentuate the need for forest areas for these mammal species, since species that use the matrix tend to require smaller amounts of forest to persist (Arroyo-Rodriguez et al. 2020).

Overall, our study contrasts with some studies that did not corroborate the HAH, such as the experimental study with plants and microarthropods performed by Haddad et al. (2016). A possible explanation for the results found by Haddad et al. (2016) is that they detected a smaller richness due to the high turnover of species in the studied landscapes, which would lead to a decline in species richness (see De Camargo et al. 2018). Another factor that can be determinant is the matrix type surrounding the patch. For instance, a study with insectivorous birds in the Amazon found that bird richness was predicted mainly by the fragment size and not by habitat amount, which can be justified by the aquatic matrix that substantially contrasts with the birds' habitat and the low dispersion capacity of the species analyzed (Bueno and Peres 2019). Here, we did not include islands in the database, but we suggest that future studies should investigate this relationship.

Effects of fragmentation per se

Our results showed that fragmentation per se had no effect on medium and large-sized mammal richness. Even for groups for which edge density and number of patches had a relatively high importance, these effects were insignificant when removing the effects of forest cover, except for herbivore richness, which was negatively affected by the number of patches in the landscape. This result corroborates previous evidence that the effects of fragmentation per se are in general non-significant (Fahrig 2003, 2017), implying that medium to large-bodied Atlantic Forest mammals respond more strongly to habitat loss than to fragmentation. On the other hand, other studies have found strong effects of fragmentation per se on mammal richness. For example, Regolin et al. (2020) found positive effects of landscape configuration, measured as edge density, on terrestrial forest mammals in the southwestern region of Brazil, whereas Palmeirim et al. (2019) unveiled that the number of patches positively affected patterns of small mammal species richness. Considering the ongoing debate on the effects of habitat fragmentation, it is important to understand under which circumstances, for which group and type of landscapes the fragmentation effects are more important. Our results contribute by adding more evidence that fragmentation has weak effects for large-bodied mammals in the Atlantic Forest and emphasizes the greater importance of landscape forest cover over landscape configuration in explaining richness patterns of forest-dweller mammal assemblages in forest fragments of the threatened Atlantic forest. We therefore reinforce the importance of focusing conservation efforts on all habitat patches, even if they are small and regardless of how they are distributed in the landscape (Fahrig et al. 2019). This is truly important for the Atlantic Forest, which is highly fragmented and has more than 80% of its remaining area in patches smaller than < 50 ha (Ribeiro et al. 2009). We also highlight the need to recover degraded areas, to increase the habitat amount in the landscape. These approaches would maximize the habitat amount available, maintaining the minimum conditions necessary to ensure high richness of mammals and also favor the persistence of other groups that occur in the Atlantic Forest (see Morante-Filho et al. 2020).

Additionally, we suggest that future studies include other features of the landscape that tend to interact with fragmentation, as this knowledge can maximize species retention in fragmented landscapes (Lees and Peres 2009; Miller-Rushing et al. 2019). For example, with the intense landscape modification, habitat remnants end up immersed within different land use types, and several studies have demonstrated the effect of matrix quality on species persistence (Brady et al. 2011; Beca et al. 2017). Finally, we agree that this is a relevant debate for conservation. Particularly, it is essential to enhance our understanding regarding the circumstances under which fragmentation per se affects biodiversity, and, when these effects are detected, whether they are mostly positive or negative. This knowledge can thus be translated into effective and vital conservation actions (Fletcher Jr et al. 2018; Fahrig et al. 2019).

Conclusions

Our results showed that mammal species richness responds more strongly to habitat amount in the surrounding landscapes and that fragmentation per se affected only herbivores, whose richness decreased with increasing number of patches. Thus, these results reinforce the HAH and support the idea that fragmentation per se has consistently weak effects on the ecological responses of species when the habitat amount is controlled (see Fahrig 2013, 2017). Understanding the responses of mammal assemblages to changes in their habitat is essential to define better conservation and management strategies for the Brazilian Atlantic Forest. These results contribute to simplification in decision making policy conservation actions, since efforts can focus on preventing habitat loss, as well as increasing or maintaining the total habitat amount in the landscape and restoring degraded habitats. These measures have direct implications for safeguard richer mammal assemblages, and this is especially important for the Atlantic Forest that has already been extensively devastated (Ribeiro et al. 2009) and has a large number of species either locally extinct or severely threatened with extinction at the national level (MMA 2014).

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Data availability

Data will be available from the Figshare Repository.

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Landscape Ecology

Supplementary Material of the manuscript: Testing the habitat amount hypothesis and fragmentation effects for medium- and large-sized mammals in a biodiversity hotspot

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Appendix S1. Supplementary Literature Cited – List of the studies used in the research. The studies were obtained from the “ATLANTIC-CAMTRAPS” datapaper” (Lima et al., 2017) and from the Scopus and Google Scholar databases.

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Table S1 – Mammal species evaluated in this study. We used Paglia et al., (2012) for weight classification, Magioli et al., (2015) for diet classification (trophic guild) and Emmons & Feer, (1997); Souza et al., (2019) and IUCN, (2019) for habitat classification. Abbreviations: (FD) forest-dependent species, (DT) disturbance-tolerant species, (Ca) carnivore, (In) insectivore, (Fr) frugivore, (On) omnivore (Hb), herbivore grazer.

Taxon	**Common name**	**Weight**	**Trophic Guild**	**Habitat**
Primates				
Atelidae				
Alouatta belzebul (Linnaeus, 1766)	Red-handed Howler Monkey	4.85-8kg	Fr	DT
Alouatta guariba (Humboldt, 1812)	Brown Howler Monkey		Fr	DT
Brachyteles arachnoides (É. Geoffroy, 1806)	Southern Muriqui	9.4-12.1kg	Fr	FD
Brachyteles hypoxanthus (Kuhl, 1820)	Northern Muriqui	13kg	Fr	FD
Callitrichidae				
Callithrix flaviceps (Thomas, 1903)	Buffy-headed Marmoset	400g	Fr/In	DT
Callithrix geoffroyi (Humboldt, 1812)	Geoffroy's Tufted-ear Marmoset	230-350kg	Fr/In	DT
Callithrix aurita (É. Geoffroy, 1812)	Buffy-tufted-ear Marmoset	400g	Fr/In	DT
Callithrix jacchus (Linnaeus, 1758)	Common Marmoset	230-350kg	Fr/In	DT
Callithrix penicillata (É. Geoffroy, 1812)	Black-pencilled Marmoset	250g	Fr/In	DT
Pitheciidae				
Callicebus personatus (É. Geoffroy, 1812)	Atlantic Titi	970-1650g	Fr	FD
Callicebus nigrifrons (Spix, 1823)	Black-fronted Titi Monkey	1300g	Fr	DT

Callicebus coimbrai (Kobayashi & Langguth, 1999)	Coimbra-Filho's Titi Minkey	1020g	Fr	FD
Callicebus melanochir (Wied-Neuwied, 1820)	Black-handed Titi	1370g	Fr	DT
Cebidae				
Sapajus nigritus (Goldfuss, 1809)	Black-horned Capuchin	3-4kg	Fr/On	DT
Sapajus robustus (Kuhl, 1820)	Crested Capuchin	2.4-3.6kg	Fr/On	DT
Sapajus libidinosus (Spix, 1823)	Bearded Capuchin	1.5-4kg	Fr/On	DT
Sapajus flavius (Schreber, 1774)	Blonde Capuchin	2.5kg	Fr/On	DT
Sapajus xanthosternos (Wied-Neuwied, 1826)	Buff-headed Capuchin	1.9-4kg	Fr/On	FD
Sapajus apella (Linnaeus, 1758)	Guianan brown tufted capuchin	13.0-4.8kg	Fr/On	DT
Rodentia				
Cuniculidae				
Cuniculus paca (Linnaeus, 1766)	Agouti	9.3kg	Fr/Hb	FD
Dasyproctidae				
Dasyprocta iacki (Feijó e Langguth, 2013)			Fr	FD
Dasyprocta azarae (Lichtenstein, 1823)	Azara’s Agouti	2.3-3.5kg	Fr	FD
Dasyprocta leporina (Linnaeus, 1758)	Red-rumped Agouti	3-8kg	Fr	FD
Sciuridae				
Guerlinguetus spp	Squirrel	120-190g	Fr	FD
Cingulata				
Dasypodidae				
Dasypus novemcinctus (Linnaeus, 1758)	Nine-Banded Armadillo	3.65kg	In/On	FD

Dasypus septemcinctus (Linnaeus, 1758)	Brazilian Lesser Long-nosed Armadillo	1.5kg	In/On	DT
Dasypus hybridus (Desmarest, 1804)	Southern Long-nosed Armadillo	1.5kg	In/On	FD
Chlamyphoridae				
Euphractus sexcinctus (Linnaeus, 1758)	Yellow Armadillo	5.4kg	In/On	DT
Priodontes maximus (Kerr, 1792)	Giant Armadillo	26.8kg	-	FD
Cabassous tatouay (Desmarest, 1804)	Greater Naked-tailed Armadillo	5.35kg	-	FD
Cabassous unicinctus (Linnaeus, 1758)	Southern Naked-tailed Armadillo	3.2kg	-	DT
Lagomorpha				
Leporidae				
Sylvilagus brasiliensis (Linnaeus, 1758)	Tapeti	1.2kg	Hb	FD
Cetartiodactyla				
Cervidae				
Mazama americana (Erxleben, 1777)	Red Brocket	24-48kg	Fr/Hb	FD
Mazama gouazoubira (G. Fischer, 1814)	Gray Brocket Deer	17-25kg	Fr/Hb	FD
Mazama nana (Hensel, 1872)	Brazilian Dwarf Brocket	15-20kg	Fr/Hb	FD
Tayassuidae				
Pecari tajacu (Linnaeus, 1758)	Collared Peccary	17-35kg	Fr/Hb	FD
Tayassu pecari (Link, 1795)	White-lipped Peccary	25-45kg	Fr/Hb	FD
Perissodactyla				
Tapiridae				
Tapirus terrestris (Linnaeus, 1758)	Tapir	260kg	Hb/Fr	FD
Pilosa				

Myrmecophagidae				
Tamandua tetradactyla (Linnaeus, 1758)	Southern Tamandua	5.2kg	-	FD
Carnivora				
Mustelidae				
Eira barbara (Linnaeus, 1758)	Tayra	4-10kg	Ca	FD
Galictis cuja (Molina, 1782)	Lesser Grison	1-3kg	Ca	DT
Procyonidae				
Nasua nasua (Linnaeus, 1766)	South American Coati	5.1kg	Fr/On	FD
Potos flavus (Schreber, 1774)	Kinkajou	2.6kg	Fr/On	FD
Procyon cancrivorus (G. Cuvier, 1798)	Crab-eating Raccoon	5.4kg	Fr/On	FD
Canidae				
Cerdocyon thous (Linnaeus, 1766)	Crab-eating Fox	6.5kg	In/On	DT
Felidae				
Panthera onca (Linnaeus, 1758)	Jaguar	61-158kg	Ca	FD
Puma concolor (Linnaeus, 1771)	Puma	22-70kg	Ca	FD
Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi	3-6kg	Ca	DT
Leopardus pardalis (Linnaeus, 1758)	Ocelot	11kg	Ca	FD
Leopardus guttulus (Hensel, 1872)	Southern Tiger Cat		Ca	FD
Leopardus tigrinus (Schreber, 1775)	Northern Tiger Cat	1.5-3kg	Ca	FD
Leopardus wiedii (Schinz, 1821)	Margay	3-9kg	Ca	FD
Mephitidae				
Conepatus semistriatus (Boddaert, 1785)	Striped Hog-nosed Skunk	2.4kg	In/On	DT

Didelphimorphia				
Didelphidae				
Didelphis aurita (Wied-Neuwied, 1826)	Southeastern Common Opossum	670-1800g	Fr/On	FD
Didelphis albiventris (Lund, 1840)	White-eared Opossum	500-2700g	Fr/On	DT

Table S2 - Akaike Information Criteria (AIC) of the variables forest cover, edge density and number of patches analyzed in relation to overall species richness, forest-dependent species, forest-tolerant species and tropic guilds richness of medium and large-sized mammals in the Atlantic Forest. In bold, the lower values of the AIC are highlighted. The value in parentheses represents the scale analyzed.

Richness	**Variables**									
	Forest cover									
	(500 m)		(1 km)		(2 km)		(4 km)		(6 km)	
	AIC	β	AIC	β	AIC	β	AIC	β	AIC	β
All species	1016.195	1.034	**1015.103**	0.981	1019.468	0.917	1023.225	0.878	1027.548	0.844
Forest-dependent	925.664	1.375	**923.294**	1.301	927.258	1.231	931.981	1.177	936.335	1.151
Disturbance-tolerant	**681.169**	0.394	682.229	0.320	683.614	0.235	684.094	0.200	684.785	0.125
Carnivore	**612.169**	1.567	619.821	1.173	622.992	1.028	623.673	1.021	625.521	0.992
Insectivore	542.639	0.215	**541.832**	0.251	542.631	0.237	542.631	0.211	543.125	0.181
Frugivore	777.308	1.119	**766.184**	1.135	770.855	1.080	777.072	1.030	784.673	0.991
Omnivore	740.212	0.553	737.688	0.570	737.695	0.571	**737.060**	0.594	737.955	0.600
Herbivore	504.418	1.823	**495.973**	1.824	501.039	1.660	508.840	1.480	514.782	1.377
	Edge density									

	(500 m)		(1 km)		(2 km)		(4 km)		(6 km)	
	AIC	β	AIC	β	AIC	β	AIC	β	AIC	β
All species	1022.707	-0.010	**1017.626**	-0.013	1023.098	-0.013	1031.915	-0.012	1038.343	-0.011
Forest-dependent	946.842	-0.010	**943.815**	-0.013	948.639	-0.013	955.444	-0.012	959.532	-0.010
Disturbance-tolerant	665.044	-0.010	**660.132**	-0.013	660.695	-0.014	664.901	-0.015	671.211	-0.013
Carnivore	626.007	-0.011	**619.051**	-0.017	620.047	-0.018	628.172	-0.014	631.433	-0.012
Insectivore	**532.589**	-0.007	533.799	-0.007	536.383	-0.007	537.965	-0.007	540.405	-0.005
Frugivore	787.211	-0.011	**786.902**	-0.013	795.137	-0.013	802.222	-0.013	810.727	-0.011
Omnivore	**733.333**	-0.008	735.233	-0.008	741.717	-0.007	747.390	-0.005	750.444	-0.003
Herbivore	514.458	-0.017	**508.873**	-0.022	511.357	-0.023	513.594	-0.025	517.445	-0.025
					Number of patches					
	(500 m)		(1 km)		(2 km)		(4 km)		(6 km)	
	AIC	β	AIC	β	AIC	β	AIC	β	AIC	β
All species	1033.924	-0.153	1015.989	-0.073	**1008.950**	-0.024	1015.745	-0.006	1028.538	-0.002
Forest-dependent	953.906	-0.162	937.726	-0.080	**932.962**	-0.025	937.610	-0.006	946.150	-0.002

Forest-tolerant	675.062	-0.139	670.649	-0.056	**667.573**	-0.018	671.451	-0.004	679.390	-0.001
Carnivore	626.541	-0.215	613.811	-0.109	**609.666**	-0.034	614.276	-0.008	623.331	-0.003
Insectivore	540.840	-0.068	541.030	-0.021	**540.151**	-0.007	540.568	-0.001	542.839	-0.000
Frugivore	805.167	-0.159	776.817	-0.082	**772.782**	-0.025	779.428	-0.006	792.587	-0.002
Omnivore	743.958	-0.097	742.341	-0.035	742.236	-0.010	**741.207**	-0.003	745.887	-0.001
Herbivore	521.829	-0.293	498.494	-0.154	**486.085**	-0.050	499.661	-0.011	511.070	-0.004

Table S3 – Variance Inflation Factor (VIF) of the analyzed variables. The value in parentheses represents the scale of effect

Richness	**Variables**			
	Patch size	Forest cover	Edge density	Number of patches
		(1 km)	(1 km)	(2 km)
All species	1.230645	2.059045	1.868206	2.896364
		(1 km)	(1 km)	(2 km)
Forest-dependent	1.226220	2.086806	1.879160	2.926779
		(500 m)	(1 km)	(2 km)
Disturbance-tolerant	1.198388	1.812274	1.911112	2.799478
		(500 m)	(1 km)	(2 km)
Carnivore	1.187137	1.825484	1.891936	2.783661
		(1 km)	(500 m)	(2 km)
Insectivore	1.217020	2.029583	1.683516	2.327059
		(1 km)	(1 km)	(2 km)
Frugivore	1.218976	2.148732	1.926149	2.980620
		(4 km)	(500 m)	(4 km)
Omnivore	1.297864	2.248158	1.819802	2.639079
		(1 km)	(1 km)	(2 km)
Herbivore	1.201581	2.093222	1.855564	2.787847

Table S4 – Slope coefficients for models the 15 possible combinations of explanatory variables plus the null models and the corresponding AIC values. (PS) patch size, (FC) forest cover, (ED) edge density and (NP) number of patches. NA means that a given explanatory variable was not included in the model.

All species

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight
FC	2.16	NA	0.2903	NA	NA	5	-479.291	969	0	0.28
FC+NP	2.148	NA	0.2343	NA	-0.09865	6	-478.381	969.3	0.33	0.237
FC+ED	2.162	NA	0.2697	-0.05162	NA	6	-478.903	970.3	1.38	0.141
PS+FC	2.16	0.01672	0.2814	NA	NA	6	-479.237	971	2.05	0.101
FC+ED+NP	2.149	NA	0.2338	-0.01421	-0.08948	7	-478.358	971.4	2.47	0.082
PS+FC+NP	2.148	0.003444	0.2331	NA	-0.09766	7	-478.379	971.5	2.51	0.08
PS+FC+ED	2.161	0.008679	0.2659	-0.0497	NA	7	-478.89	972.5	3.53	0.048
PS+FC+ED+NP	2.149	0.002374	0.233	-0.01387	-0.08902	8	-478.357	973.6	4.68	0.027
NP	2.196	NA	NA	NA	-0.2469	5	-484.181	978.7	9.78	0.002
PS+NP	2.193	0.04827	NA	NA	-0.2217	6	-483.702	979.9	10.98	0.001
ED+NP	2.199	NA	NA	-0.02305	-0.2314	6	-484.122	980.8	11.82	0.001
PS+ED+NP	2.195	0.04706	NA	-0.01626	-0.2115	7	-483.673	982.1	13.1	0
PS+ED	2.247	0.08443	NA	-0.122	NA	6	-487.396	987.3	18.36	0

ED	2.263	NA	NA	-0.1544	NA	5	-488.958	988.3	19.34	0
PS	2.257	0.1169	NA	NA	NA	5	-489.635	989.6	20.69	0
Null	2.289	NA	NA	NA	NA	4	-492.993	994.2	25.28	0

Forest-dependent

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight
FC	1.807039	NA	0.392685	NA	NA	5	-445.725	901.8249	0	0.314002
FC+NP	1.793328	NA	0.329722	NA	-0.10751	6	-444.97	902.4681	0.643154	0.227653
FC+ED	1.808652	NA	0.375124	-0.04151	NA	6	-445.549	903.6267	1.801763	0.127551
PS+FC	1.807077	0.004852	0.389987	NA	NA	6	-445.722	903.973	2.14807	0.107272
PS+FC+NP	1.79271	-0.00935	0.333402	NA	-0.11023	7	-444.957	904.6221	2.797175	0.077541
FC+ED+NP	1.792768	NA	0.329942	0.004596	-0.11049	7	-444.969	904.646	2.82105	0.076621
PS+FC+ED	1.808612	-0.00152	0.375846	-0.04186	NA	7	-445.549	905.8067	3.981747	0.042885
PS+FC+ED+NP	1.792323	-0.00911	0.33347	0.003358	-0.11233	8	-444.956	906.8292	5.004271	0.02572
NP	1.866183	NA	NA	NA	-0.31079	5	-452.461	915.2974	13.47248	0.000373
PS+NP	1.862683	0.050643	NA	NA	-0.28394	6	-452.079	916.6853	14.8604	0.000186
ED+NP	1.867392	NA	NA	-0.01245	-0.30234	6	-452.449	917.426	15.60104	0.000129
PS+ED+NP	1.863182	0.050283	NA	-0.00474	-0.28093	7	-452.077	918.8619	17.03699	6.27E-05
PS+ED	1.932055	0.09786	NA	-0.14464	NA	6	-456.671	925.8699	24.04494	1.89E-06
ED	1.952227	NA	NA	-0.18323	NA	5	-458.189	926.7538	24.92885	1.21E-06

PS	1.947117	0.136035	NA	NA	NA	5	-458.85	928.0759	26.25099	6.26E-07
Null	1.987223	NA	NA	NA	NA	4	-462.13	932.5089	30.68393	6.82E-08

Disturbance-tolerant

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight
FC	0.926639	NA	0.124702	NA	NA	5	-291.038	592.4516	0	0.256505
FC+ED	0.9241	NA	0.112199	-0.05394	NA	6	-290.743	594.014	1.562386	0.117443
FC+NP	0.921427	NA	0.109838	NA	-0.03823	6	-290.944	594.4168	1.965125	0.096023
PS+FC	0.924245	0.016628	0.120467	NA	NA	6	-291.001	594.5301	2.078459	0.090733
NP	0.931623	NA	NA	NA	-0.11201	5	-292.32	595.0148	2.563138	0.071206
Null	0.957575	NA	NA	NA	NA	4	-293.432	595.1134	2.661789	0.067779
ED	0.947507	NA	NA	-0.08936	NA	5	-292.55	595.4758	3.024191	0.056546
PS+FC+ED	0.923484	0.005252	0.111198	-0.05241	NA	7	-290.739	596.1876	3.73593	0.039614
FC+ED+NP	0.924239	NA	0.112528	-0.05448	0.001183	7	-290.743	596.1945	3.742824	0.039478
PS	0.946924	0.050183	NA	NA	NA	5	-293.069	596.5128	4.061123	0.033669
PS+FC+NP	0.920427	0.010673	0.108615	NA	-0.03435	7	-290.93	596.5682	4.116576	0.032749
ED+NP	0.933819	NA	NA	-0.04458	-0.08155	6	-292.182	596.8926	4.440949	0.027846
PS+NP	0.929262	0.022442	NA	NA	-0.10211	6	-292.254	597.0367	4.585015	0.02591
PS+ED	0.942956	0.029151	NA	-0.07928	NA	6	-292.437	597.4029	4.951222	0.021575

PS+FC+ED+NP	0.923739	0.005448	0.111851	-0.05349	0.002451	8	-290.739	598.3954	5.943747	0.013135
PS+ED+NP	0.931826	0.018678	NA	-0.04141	-0.07543	7	-292.137	598.9835	6.531902	0.009788

Carnivore

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight
FC	0.498454	NA	0.421698	NA	NA	5	-287.232	584.8386	0	0.327781
PS+FC	0.48549	0.07142	0.393442	NA	NA	6	-286.809	586.1468	1.308161	0.17042
FC+NP	0.480179	NA	0.364143	NA	-0.11425	6	-286.827	586.1822	1.343612	0.167426
FC+ED	0.498315	NA	0.409868	-0.03228	NA	6	-287.178	586.8848	2.046202	0.11783
PS+FC+NP	0.474488	0.056059	0.354795	NA	-0.08858	7	-286.586	587.88	3.041405	0.071639
FC+ED+NP	0.477	NA	0.364024	0.027054	-0.1342	7	-286.801	588.3118	3.473208	0.057728
PS+FC+ED	0.485953	0.069255	0.390012	-0.01163	NA	7	-286.803	588.3143	3.475672	0.057657
PS+FC+ED+NP	0.469888	0.058376	0.354295	0.035614	-0.11379	8	-286.542	590.0014	5.162782	0.024803
NP	0.508061	NA	NA	NA	-0.34783	5	-292.349	595.0729	10.2343	0.001964
PS+NP	0.49388	0.091837	NA	NA	-0.29628	6	-291.693	595.9142	11.07561	0.00129
ED+NP	0.504842	NA	NA	0.031016	-0.37047	6	-292.315	597.1586	12.31997	0.000692
PS+ED+NP	0.488842	0.094368	NA	0.043705	-0.3268	7	-291.627	597.9634	13.12477	0.000463
PS	0.547118	0.17703	NA	NA	NA	5	-295.034	600.4425	15.60393	0.000134
PS+ED	0.542989	0.146497	NA	-0.12115	NA	6	-294.269	601.0653	16.22673	9.82E-05
ED	0.581562	NA	NA	-0.17598	NA	5	-296	602.3744	17.53583	5.10E-05

Null	0.604296	NA	NA	NA	NA	4	-297.793	603.834	18.9954	2.46E-05

Insectivore

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight
ED	0.801887	NA	NA	-0.10726	NA	4	-256.58	521.4087	0	0.152208
Null	0.833036	NA	NA	NA	NA	3	-257.664	521.4765	0.067811	0.147134
PS+ED	0.803881	-0.08369	NA	-0.13076	NA	5	-255.826	522.0278	0.619132	0.111685
FC	0.815015	NA	0.064221	NA	NA	4	-257.268	522.784	1.375258	0.076525
PS	0.839803	-0.05528	NA	NA	NA	4	-257.327	522.903	1.494325	0.072102
ED+NP	0.814783	NA	NA	-0.13662	0.072026	5	-256.298	522.9703	1.561574	0.069718
FC+ED	0.798646	NA	0.022766	-0.09763	NA	5	-256.539	523.4525	2.043809	0.054781
PS+FC	0.817041	-0.08263	0.091931	NA	NA	5	-256.581	523.5376	2.128925	0.052499
NP	0.831824	NA	NA	NA	-0.00439	4	-257.663	523.574	2.165335	0.051551
PS+FC+ED	0.798017	-0.094	0.048585	-0.1127	NA	6	-255.641	523.81	2.401278	0.045815
PS+ED+NP	0.812158	-0.07613	NA	-0.14649	0.045414	6	-255.72	523.9685	2.559828	0.042323
FC+NP	0.821349	NA	0.086403	NA	0.047513	5	-257.148	524.6709	3.262243	0.029789
FC+ED+NP	0.810427	NA	0.054218	-0.12328	0.097106	6	-256.102	524.7324	3.323647	0.028888
PS+NP	0.832609	-0.06243	NA	NA	-0.0286	5	-257.272	524.9199	3.51118	0.026302
PS+FC+ED+NP	0.807079	-0.08654	0.071891	-0.13013	0.076079	7	-255.377	525.4635	4.054756	0.020043
PS+FC+NP	0.820572	-0.07933	0.104041	NA	0.028107	6	-256.54	525.6088	4.200107	0.018638

Frugivore

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight
FC	1.518435	NA	0.317985	NA	NA	5	-359.685	729.7443	0	0.28022
FC+NP	1.509277	NA	0.272706	NA	-0.08339	6	-358.919	730.366	0.621723	0.205349
PS+FC	1.516767	0.038198	0.297948	NA	NA	6	-359.226	730.9804	1.236145	0.151033
FC+ED	1.519946	NA	0.303222	-0.03451	NA	6	-359.465	731.4581	1.713805	0.118946
PS+FC+NP	1.509232	0.028928	0.263047	NA	-0.07317	7	-358.666	732.0409	2.296649	0.088877
FC+ED+NP	1.509415	NA	0.272637	-0.00116	-0.0826	7	-358.919	732.5462	2.801919	0.069035
PS+FC+ED	1.518248	0.034242	0.289103	-0.02559	NA	7	-359.111	732.9303	3.185993	0.056973
PS+FC+ED+NP	1.508754	0.029192	0.263159	0.003603	-0.07553	8	-358.664	734.2459	4.501581	0.029512
PS+NP	1.547555	0.07365	NA	NA	-0.226	6	-367.873	748.2745	18.53019	2.65E-05
NP	1.556117	NA	NA	NA	-0.26806	5	-369.549	749.4722	19.72794	1.46E-05
PS+ED+NP	1.547667	0.073568	NA	-0.00113	-0.22526	7	-367.873	750.4547	20.71041	8.92E-06
ED+NP	1.556984	NA	NA	-0.01384	-0.25841	6	-369.523	751.5742	21.82994	5.10E-06
PS+ED	1.59451	0.109348	NA	-0.11167	NA	6	-372.759	758.0463	28.30199	2.00E-07
PS	1.601941	0.138151	NA	NA	NA	5	-375.113	760.6012	30.85686	5.58E-08
ED	1.619475	NA	NA	-0.15617	NA	5	-376.516	763.4065	33.66216	1.37E-08
Null	1.648786	NA	NA	NA	NA	4	-381.645	771.5378	41.79347	2.36E-10

Omnivore

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight
FC	1.365114	NA	0.137192	NA	NA	5	-337.241	684.8562	0	0.147986
ED	1.388197	NA	NA	-0.12014	NA	5	-337.291	684.9565	0.100316	0.140746
FC+ED	1.365555	NA	0.092608	-0.08044	NA	6	-336.312	685.1517	0.295536	0.127657
PS+FC	1.361688	-0.05631	0.172311	NA	NA	6	-336.645	685.8187	0.962532	0.091455
PS+FC+ED	1.360977	-0.06075	0.128261	-0.08461	NA	7	-335.615	685.9387	1.082547	0.086129
FC+ED+NP	1.376165	NA	0.131118	-0.11008	0.087558	7	-335.652	686.0119	1.155724	0.083034
FC+NP	1.369521	NA	0.159697	NA	0.035638	6	-337.111	686.7503	1.894074	0.057402
PS+ED	1.390447	-0.02224	NA	-0.12727	NA	6	-337.178	686.8846	2.02845	0.053672
ED+NP	1.394317	NA	NA	-0.13494	0.028454	6	-337.204	686.9372	2.081007	0.05228
PS+FC+ED+NP	1.371524	-0.0558	0.16055	-0.11108	0.079628	8	-335.072	687.0611	2.204916	0.049139
PS+FC+NP	1.36548	-0.05416	0.18839	NA	0.027568	7	-336.568	687.8458	2.989597	0.033192
Null	1.411681	NA	NA	NA	NA	4	-339.97	688.1877	3.331534	0.027976
PS+ED+NP	1.394668	-0.01837	NA	-0.13707	0.021248	7	-337.133	688.9757	4.119506	0.018866
NP	1.393835	NA	NA	NA	-0.05453	5	-339.508	689.3917	4.535526	0.015323
PS	1.409796	0.008895	NA	NA	NA	5	-339.951	690.2767	5.420475	0.009844
PS+NP	1.394232	-0.00829	NA	NA	-0.05831	6	-339.494	691.5161	6.659958	0.005297

Herbivore

Model	(Int)	PS	FC	ED	NP	df	logLik	AICc	Delta	Weight

FC+NP	0.11201	NA	0.375164	NA	-0.42738	6	-228.267	469.0629	0	0.501534
FC+ED+NP	0.10401	NA	0.382069	0.064822	-0.47867	7	-228.115	470.9396	1.87665	0.196242
PS+FC+NP	0.11616	0.034229	0.36307	NA	-0.41309	7	-228.141	470.9918	1.928875	0.191184
PS+FC+ED+NP	0.107115	0.040091	0.36865	0.074365	-0.46972	8	-227.946	472.8097	3.746782	0.077037
FC	0.175697	NA	0.591169	NA	NA	5	-233.394	477.163	8.100058	0.008738
FC+ED	0.176993	NA	0.525609	-0.13074	NA	6	-232.481	477.4903	8.427357	0.007419
PS+FC	0.178124	0.082601	0.544047	NA	NA	6	-232.649	477.8255	8.762626	0.006274
PS+FC+ED	0.180311	0.064861	0.499436	-0.10964	NA	7	-232.043	478.7943	9.73142	0.003865
NP	0.171518	NA	NA	NA	-0.6981	5	-234.427	479.2282	10.16524	0.003111
PS+NP	0.169082	0.0896	NA	NA	-0.63853	6	-233.548	479.6249	10.562	0.002551
ED+NP	0.170258	NA	NA	0.027939	-0.72053	6	-234.398	481.3242	12.26126	0.001091
PS+ED+NP	0.164393	0.094916	NA	0.055283	-0.68017	7	-233.441	481.5902	12.52731	0.000955
PS+ED	0.323386	0.183493	NA	-0.27039	NA	6	-243.783	500.0943	31.03134	9.16E-08
ED	0.352448	NA	NA	-0.35845	NA	5	-247.254	504.8839	35.82101	8.35E-09
PS	0.347089	0.257859	NA	NA	NA	5	-247.766	505.9069	36.84401	5.01E-09
Null	0.442161	NA	NA	NA	NA	4	-255.124	518.4964	49.43344	9.25E-12

Table S5 – Coefficients and significance values for the average model. Significant values are highlighted in **bold**. Estimate: the effect (slope) of the explanatory variable; Std. Error: standard error for the estaime; Adjusted SE: adjsuted standard error: Pr(>|z|): p-value, obtained from the z-value.

Variable	**Full average**					**Conditional average**				
All species	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
(Intercept)	2.155359	0.175356	0.176690	12.199	< 2e-16	2.155359	0.175356	0.176690	12.199	< 2e-16
Patch size	0.002519	0.025889	0.026078	0.097	0.923062	0.009789	0.050339	0.050717	0.193	0.847
Forest cover	0.260027	0.068237	0.068656	3.787	**0.000152**	0.261198	0.066115	0.066549	3.925	**8.68e-05**
Edge density	-0.011212	0.039305	0.039530	0.284	0.776686	-0.037558	0.064695	0.065153	0.576	0.564
Number of patches	-0.041954	0.070517	0.070794	0.593	0.553437	-0.097518	0.078358	0.078937	1.235	0.217
Forest-dependent										

(Intercept)	1.8016561	0.1708142	0.1721132	10.468	< 2e-16	1.801656	0.170814	0.1721	10.468	< 2e-16
Patch size	-0.0004915	0.0293029	0.0295241	0.017	0.987	-0.001938	0.058156	0.0586	3.30E-02	0.974
Forest cover	0.3638762	0.0797253	0.0802469	4.534	**5.80E-06**	0.364151	0.079126	0.0797	4.572	**4.80E-06**
Edge density	-0.0066542	0.0416925	0.0419654	0.159	0.874	-0.024377	0.077045	0.0776	0.314	0.753
Number of patches	-0.0446015	0.0795816	0.079911	0.558	0.577	-0.109241	0.091927	0.0926	1.179	0.238
Disturbance-tolerant										
(Intercept)	0.930147	0.197445	0.198942	4.675	2.90E-06	0.93015	0.19744	0.19894	4.675	2.90E-06
Patch size	0.005221	0.033114	0.033338	0.157	0.876	0.01954	0.06184	0.06229	0.314	0.754
Forest cover	0.080515	0.074172	0.07443	1.082	0.279	0.11742	0.06074	0.0612	1.919	**0.055**
Edge density	-0.019675	0.051633	0.051898	0.379	0.705	-0.06046	0.07567	0.07623	0.793	0.428
Number of patches	-0.018348	0.061159	0.06147	0.298	0.765	-0.05804	0.09761	0.09823	0.591	0.555

Carnivore										
(Intercept)	0.488815	0.251602	0.253516	1.928	0.053838	0.488815	0.251602	0.253516	1.928	0.053838
Patch size	0.021829	0.055129	0.055412	0.394	0.69363	0.066856	0.079359	0.079961	0.836	0.403098
Forest cover	0.392242	0.107164	0.107884	3.636	**0.000277**	0.394101	0.103951	0.104697	3.764	**0.000167**
Edge density	-0.00201	0.056164	0.056566	0.036	0.971675	-0.00775	0.110089	0.11088	0.07	0.944311
Number of patches	-0.03752	0.095908	0.096387	0.389	0.697112	-0.11508	0.138886	0.139901	0.823	0.410754
Insectivore										
(Intercept)	0.81584	0.13302	0.13401	6.088	<2e-16	0.81584	0.13302	0.13401	6.088	<2e-16
Patch size	-0.03005	0.05862	0.05887	0.511	0.61	-0.07718	0.07202	0.07255	1.064	0.287
Forest cover	0.02073	0.05562	0.0559	0.371	0.711	0.06341	0.08219	0.08276	0.766	0.444
Edge density	-0.06333	0.08384	0.08414	0.753	0.452	-0.12053	0.08052	0.0811	1.486	0.137

Number of patches	0.01223	0.05773	0.05806	0.211	0.833	0.04259	0.10153	0.1022	0.417	0.677
Frugivore										
(Intercept)	1.514747	0.136817	0.137858	10.988	<2e-16	1.51475	0.13682	0.13786	10.988	<2e-16
Patch size	0.011155	0.027994	0.028137	0.396	0.692	0.03417	0.04018	0.04048	0.844	0.399
Forest cover	0.29261	0.058043	0.058432	5.008	**6.00E-07**	0.29263	0.058	0.05839	5.011	**5e-07**
Edge density	-0.00554	0.031528	0.031734	0.174	0.861	-0.02017	0.05767	0.05808	0.347	0.728
Number of patches	-0.03157	0.059248	0.059501	0.531	0.596	-0.08037	0.07081	0.07135	1.126	0.260
Omnivore										
(Intercept)	1.37503	0.14743	0.14854	9.257	<2e-16	1.37503	0.14743	0.14854	9.257	<2e-16
Patch size	-0.01642	0.03902	0.0392	0.419	0.675	-0.04723	0.05408	0.05445	0.867	0.3857
Forest cover	0.09313	0.08853	0.08881	1.049	0.294	0.13776	0.0738	0.07428	1.855	0.0636

Edge density	-0.06554	0.07123	0.07146	0.917	0.359	-0.10717	0.06193	0.06236	1.719	0.0857
Number of patches	0.01489	0.05045	0.05069	0.294	0.769	0.04733	0.08097	0.08145	0.581	0.5612
Herbivore										
(Intercept)	0.11302	0.19519	0.19668	0.575	0.56553	0.11302	0.19519	0.19668	0.575	0.565533
Patch size	0.01072	0.04007	0.04032	0.266	0.79033	0.03804	0.06826	0.06877	0.553	0.580202
Forest cover	0.37536	0.11736	0.11813	3.177	**0.00149**	0.37827	0.11304	0.11384	3.323	**0.000891**
Edge density	0.01714	0.07058	0.071	0.241	0.80925	0.0598	0.12178	0.12263	0.488	0.625799
Number of patches	-0.42868	0.16106	0.16201	2.646	**0.00815**	-0.44025	0.14678	0.14785	2.978	**0.002904**

CAPÍTULO II

SPATIAL PREDICTORS AND SPECIES TRAITS: EVALUATING WHAT REALLY MATTERS FOR MEDIUM AND LARGE-SIZED MAMMALS IN THE ATLANTIC FOREST

Artigo aceito para publicação na Mammal Review

Spatial predictors and species' traits: evaluating what really matters for medium-sized and large mammals in the Atlantic Forest, Brazil

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ABSTRACT

1. Habitat loss and the conversion of natural environments to anthropogenic land-uses are among the main drivers of biodiversity decline worldwide. The remaining habitats are inserted in highly modified landscapes, presenting contrasting patch and landscape features. Understanding species' responses to these anthropogenic land-use changes is essential for informing conservation planning.

2. We evaluate which spatial predictors (measured at the patch and landscape scales) and species' life-history traits best predict the occurrence of medium-sized and large mammals in forest fragments of the threatened Atlantic Forest of South America.

3. We gathered occurrence data for 36 medium-sized and large mammal species recorded by camera traps, distributed over 220 forest fragments spanning the entire Atlantic Forest biome. Species were classified according to their characteristics as: 'hunted forest-dependent', 'non-hunted forest-dependent' and 'generalist' species. Further, each species' occurrence was related to spatial predictors and life-history trait variables.

4. We revealed a severe defaunation of forest mammals occurring in most forest fragments in the Atlantic Forest. Landscapes containing large forest patches, low road density and high human population density harboured high numbers of mammal species, including those exhibiting greater body mass. Nevertheless, mammal groups diverge in their sensitivity to landscape changes. Hunted forest-dependent species mainly occurred in landscapes with lower edge density and numbers of patches and with less anthropogenic disturbance, while non-hunted forest-dependent species mainly occupied large forest fragments. Finally, generalist species also occurred in landscapes with low edge density and number of patches, but were more prevalent in landscapes with higher human population density.

5. We stress the importance of maintaining large forest fragments, considering the effects of landscape configuration on conservation strategies, and reducing anthropogenic disturbances to ensure a greater persistence of mammal species in the Atlantic Forest.

Keywords: anthropogenic disturbance, defaunation, habitat loss, landscape composition, landscape configuration, mammalian species' occurrence, tropical forest.

Running head: Evaluating what really matters for mammals

INTRODUCTION

Biodiversity decline is driven mainly by habitat loss and the conversion of natural habitats for agricultural expansion and urbanisation (Tilman et al. 2001, Green et al. 2005). In fact, one of the main drivers of global forest loss is deforestation for the production of commodities, followed by silviculture, shifting agriculture and forest fires (Curtis et al. 2018). The demand for land and resources has occurred at the expense of Tropical forests: 55% and 28% of agricultural land in the Tropics comes from intact and disturbed forests, respectively (Gibbs et al. 2010). As a result, the remaining habitats are immersed in highly human-modified landscapes (HMLs), with direct effects on the persistence of forest biodiversity in the long term.

Variation in the magnitude of land-use changes leads to different types of HMLs, varying in the proportion of each habitat type remaining (landscape composition) and/or presenting different spatial arrangements (landscape configuration), both exerting influence on the persistence of organisms (Dunning et al. 1992). There is an ongoing debate on whether landscape composition or configuration is more closely related to biodiversity (Andrén 1994, Fahrig 2003). For instance, landscape composition rather than configuration is more important in explaining bird occupancy in the Brazilian Atlantic

Forest (Morante-Filho et al. 2021) and phyllostomid bat communities in the Lacandona Forest in Mexico (Arroyo-Rodríguez et al. 2016). Conversely, Regolin et al. (2020) found that landscape configuration had stronger effects on mammal species richness than landscape composition within an ecotonal region in western Brazil. Thus, further studies are needed to improve our understanding of the effects of landscape composition and configuration on species' persistence so that we can propose sound conservation strategies in HMLs. In addition, HMLs are mainly composed of small habitat patches, which has pervasive consequences for species' persistence (Benchimol & Peres 2014, 2015) and makes the landscapes more susceptible to other types of human disturbances. For example, the proximity of roads and human settlements tends to facilitate access to forests by hunters, which might lead to a marked decrease in the abundance of game species, especially large mammals (Peres & Palacios 2007, Benítez-López et al. 2017).

Even within the same category, species exhibit divergent responses to landscape changes, with life-history traits greatly explaining different sensitivities to disturbance (Urquiza-Haas et al. 2009, Benchimol & Peres 2015). In particular, forest-dependent species (i.e., those that are highly dependent on forest resources) comprise the most vulnerable category, whereas generalist species (i.e., those that do not depend exclusively on forests and use also non-forest areas) exhibit lower sensitivity to disturbances and can thrive in HMLs (Pardini et al. 2009, 2010, Morante-Filho et al. 2015). Among vertebrates, medium-sized and large forest mammals comprise an excellent group to assess the impact of landscape changes on species' occurrence. Their persistence is vital for forest functioning, given the wide range of ecological roles and ecosystem services they provide, such as seed dispersal over long distances and top-down control (Galetti et al. 2001, Davidson et al. 2012, Galetti & Dirzo 2013). However, several mammal species are currently under pervasive human threats, mainly habitat loss and hunting, which have contributed to the depletion of populations and species' extinction especially in Tropical forests (Ceballos et al. 2002, Benítez-López et al. 2017). Furthermore, specific life-history characteristics, such as large body size, low reproductive rates and large home range, increase mammal extinction risks (Cardillo et al. 2005, 2008). Assessing the main drivers of mammal species' extinction in HMLs can therefore contribute to a better understanding of which groups can cope with landscape modification at different scales in Tropical forests.

The South American Atlantic Forest is considered one of the most threatened forests in the world. The remaining forest fragments are embedded within an anthropogenic matrix consisting mainly of pasture, agriculture and urban areas (Myers et al. 2000, Lira et al. 2021). Only 28% of its original area remains, mostly in the form of small and highly disturbed forest fragments (Rezende et al. 2018). Nevertheless, a total of 384 species of mammals occurs in the entire biome, comprising 262 terrestrial and arboreal species and 122 bats (Figueiredo et al. 2021), and including several species currently threatened with extinction (i.e., Critically Endangered, Endangered, or Vulnerable; IUCN 2021).

We gathered a robust dataset on medium-sized to large mammals in forest fragments distributed throughout the Brazilian Atlantic Forest to evaluate which spatial predictors and life-history traits best predict species' occurrence. Specifically, we assessed the effects of: forest loss at the patch scale (i.e., patch size) and at the landscape scale (i.e., forest cover); landscape configuration (edge density and number of patches); anthropogenic disturbances (road density and human population density); and species' traits (body mass and trophic guild) on patterns of overall and individual species' occurrence. Considering the occurrence of all species, we expected to reveal strong and positive effects of forest cover, with large species (>7 kg) and those exhibiting specialised trophic guilds (e.g., frugivores, carnivores) presenting a higher occurrence in less disturbed landscapes. In addition, we expected negative effects of anthropogenic disturbance on overall species' occurrence, given the combined importance of landscape factors and intrinsic biological characteristics to explain mammal persistence (Ripple et al. 2017, Cardillo et al. 2005). Further, we expected that species would exhibit different responses to the variables we examined, according to their ecological and habitat requirements. As previously found for medium-sized and large mammal species richness (Rios et al. 2021), we specifically predicted that: (1) occurrence of hunted forest-dependent species would be affected positively by forest cover and negatively by road density and human population, given their susceptibility to hunting (Peres & Palacios 2007, Cullen et al. 2001); (2) occurrence of non-hunted forest-dependent species would mostly be explained by positive forest cover effects, and (3) occurrence of generalist species would mainly and positively be affected by anthropogenic disturbances and landscape configuration variables, due to the great plasticity of habitat use by these species (see Appendix S1). We also expected a positive effect of patch size, as shown for mammals in other Neotropical forest landscapes (Canale et al. 2012, Michalski & Peres 2005). Finally, we classified species into 'winners' and 'losers' from disturbance, to aid effective conservation strategies for each mammal species in the threatened Atlantic Forest.

METHODS

Literature survey and study selection

Based on an extensive literature review, we gathered information on the occurrence (presence = 1; absence = 0) of each medium-sized and large terrestrial mammal species (>1 kg, Paglia et al. 2012) within forest fragments (i.e., any forest fragment >1.23 ha) throughout the Atlantic Forest. The review was concluded in May 2020, using Scopus (https://www.scopus.com/home.uri) and Google Scholar (https://scholar.google.com/) search engines. The following search term sequences were used: 'Atlantic Forest' AND 'medium-sized mammal' OR 'large-sized mammal' OR 'medium bodied mammal' OR 'large bodied mammal'. At Google Scholar we restricted our search to the first 200 results found. Additionally, we included studies from the “ATLANTIC-CAMTRAPS” (Lima et al. 2017) and “ATLANTIC MAMMALS” (Souza et al. 2019) data papers. We also included three unpublished datasets - either provided by researchers (Magioli & Morato, and Flesher) or our own data. These three datasets represented a total of 35 forest fragments located in southern Bahia state, Brazil.

We used the following criteria to include a study in our database: 1) it must present all mammal species detected within each forest fragment; 2) it must provide the geographical coordinates of each sampled forest fragment; 3) data must have been collected using camera traps deployed on the ground, an efficient and widely used sampling technique to detect terrestrial mammal species (Srbek-Araujo & Chiarello 2005), and the study should encompass a minimum sampling effort of 30 camera/day or 730 hours in order to minimise false negatives (i.e., when the species occurs in the fragment, but could not be detected due to the low sampling effort); 4) the records must have been identified at the species level. Primates and exotic and/or elusive species, such as *Bradypus torquatus*, were not included, as they are rarely detected by camera traps placed on the ground. We also excluded data that were collected on ‘real’ islands (i.e., forests surrounded by open water; Fig. 1). Though *Guerlinguetus* spp. comprise small rodent species (<1 kg, so outside our size range), they are frequently recorded on camera traps and we therefore included them in our database. However, we excluded from the analysis species presenting fewer than six records considering all forest fragments analysed in our database, such as *Speothos venaticus* and *Dasypus hybridus*, due to uncertainty about their detectability. Whenever different studies conducted camera trap surveys in the same forest fragments, we combined the information (i.e., species records and sampling effort), if the difference between the years of data collection between the studies did not exceed eight years, and if both studies met all the criteria mentioned above. Our final database consisted of 36 mammal species, with data from 69 studies distributed in 220 forest fragments (or patches), all located in the Brazilian Atlantic Forest (i.e., no study from Argentina was included; Fig. 2, Appendices S2, S3).

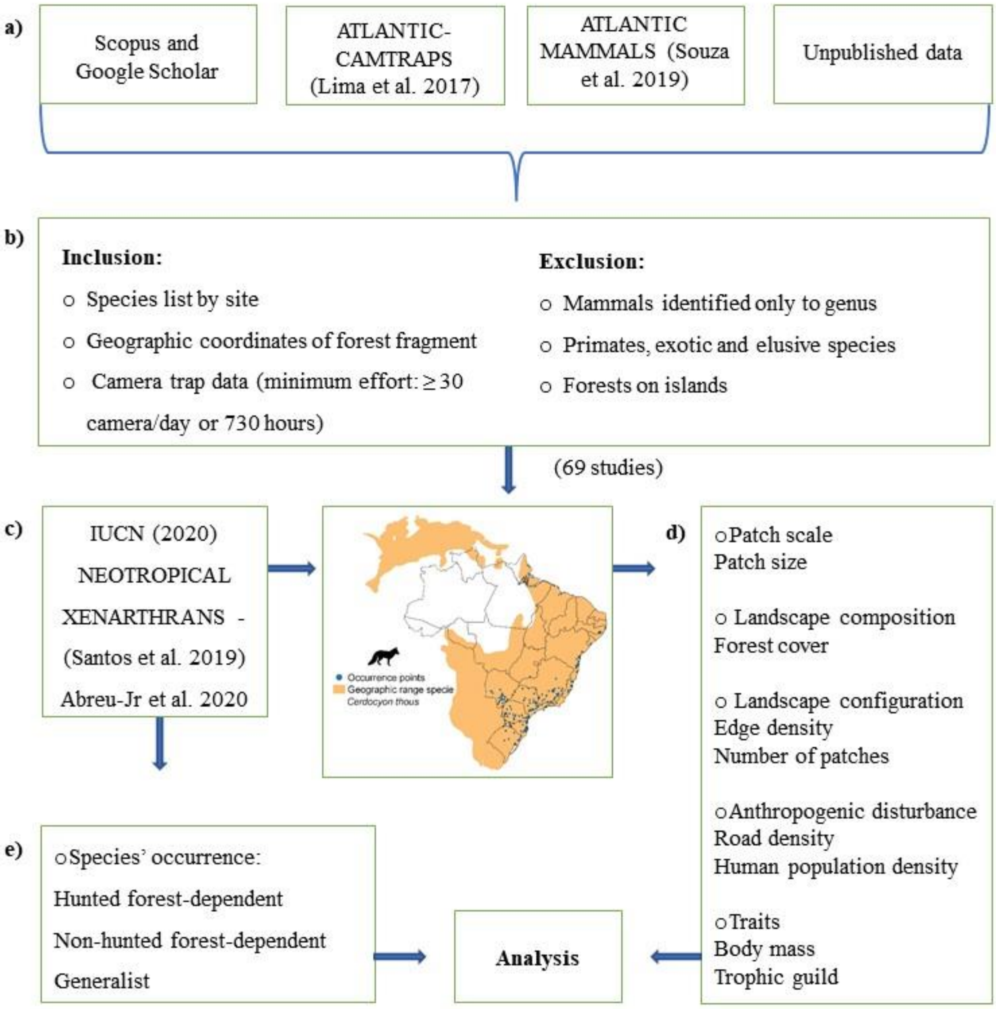


Fig. 1. Diagram showing the main methodological steps. a) Databases used to obtain mammal occurrence data; b) criteria used to filter the studies; c) literature used to elaborate the geographic range of each species and determine mammal occurrence

(presence/absence). The resulting 69 studies were used to elaborate species' geographic range; d) spatial predictors and life-history traits and e) response variable used in the analysis.

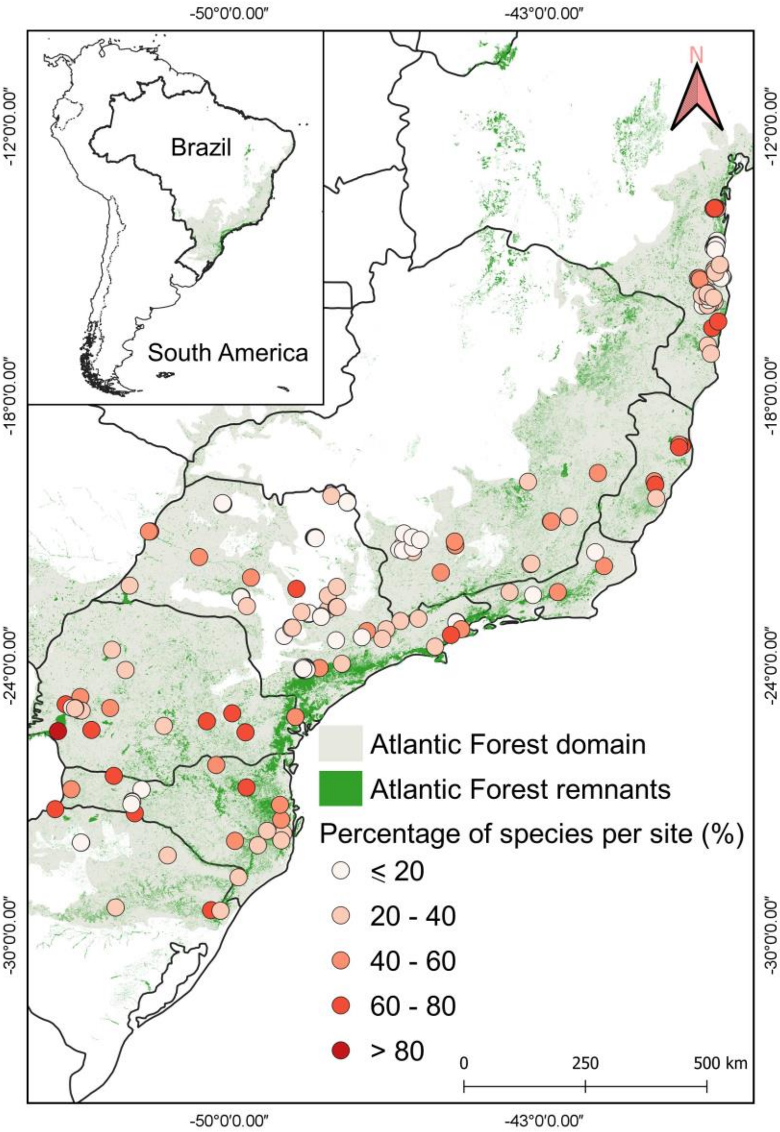


Fig. 2. Location of the 220 forest fragments where camera trap surveys on medium-sized and large mammals were conducted in the Brazilian Atlantic Forest following our criteria. The coloured circles indicate the percentage of species recorded in each forest fragment compared to what was expected.

Species' geographic ranges

To delimit the geographic range of each species, we used the polygons provided by the International Union for Conservation of Nature (IUCN 2021), in addition to information provided by the "NEOTROPICAL XENARTHRANS" dataset (Santos et al. 2019) to improve knowledge of the natural distribution of xenarthran species. Subsequently, we carefully examined each polygon, and whenever an incongruence in the geographic range was found, we amended the polygons. To do this, we used the records obtained from the studies in our database, a literature review on squirrel species (see Abreu-Jr et al. 2020), and our own knowledge of each species. Although IUCN polygons provide robust information on species' ranges and are widely used (Gonzaléz-Maya et al. 2017, Bogoni et al. 2020), they may contain some errors for certain species, which is why we deemed these amendments necessary to improve data quality. Finally, to determine our response variable – species' occurrence - we assigned '1' (i.e., presence) when the species was found in the surveyed forest fragment, and '0' (i.e., absence) for each species expected to occur in the surveyed forest fragment but not detected there.

Spatial predictors and species' life-history traits

We carefully selected metrics at different spatial scales widely known to affect forest vertebrate species in HMLs (see Benchimol & Peres 2014, Morante-Filho et al. 2021). We selected local (patch-scale) and landscape-scale metrics, in addition to anthropogenic disturbance variables for each forest fragment used in our final database (Appendix S4). At the patch scale, we evaluated patch size in hectares, which was obtained directly from the study when available or calculated using Google Earth Pro, using satellite images with a date closest to the date of data collection. Patch size ranged from 1.23 ha to 18562.6 ha (mean = 5200.5156, standard deviation ± 17549.9933). To evaluate landscape composition and configuration we applied a patch-landscape approach ((McGarigal & Cushman 2002) in which mammal occurrence was measured in the forest patches and the explanatory variables were assessed within landscaped with varying radii sizes surrounding each forest patch (see details below). To extract landscape metrics, we used maps of the MapBiomas Project (Collection 4, 2019) derived from 30 m resolution Landsat imagery, downloaded from the Brazilian Annual Land Use and Land Cover Mapping Project (available at http://mapbiomas.org) and calculated one landscape composition metric: forest cover (percentage of native forest, excluding agroforestry); and two landscape configuration metrics: edge density (total perimeter of all forest fragments divided by the buffer size), and the number of forest patches within each buffer. For these metrics, we used maps corresponding to the year in which surveys were performed for each study. We also calculated two metrics related to anthropogenic disturbance: road density (measured as the total length of roads divided by the buffer size), and human population density (extracted by the Brazilian Institute of Geography and Statistics from a census performed in 2010). We opted for using data from 2010, since it comprises an intermediate year among data collection of all compiled studies. Each spatial predictor was calculated using buffer sizes of 0.5, 1, 2, 4 and 6 km radius around the sampling point provided by each study, to take into account the scale of effect (i.e., the spatial extent at which a given landscape feature has a greater relationship with the dependent variable; Fahrig 2013). The radius sizes were defined *a priori* based on previous studies on medium-sized and large mammals in the Atlantic Forest (Lyra-Jorge et al. 2010, Beca et al. 2017, Regolin et al. 2017). Spatial variables were calculated in R 3.5.2 (R Core Team 2018) using the package *landscapemetrics* (Hesselbarth et al. 2019) or in QGIS 3.4.

As well as spatial predictors, we used species' life-history traits to assess their role in explaining patterns of species' occurrence, since these traits can be good indicators of species' susceptibility to environmental changes (Cardillo et al. 2005, Bogoni et al. 2020). In particular, diet quality and body mass are usually related to each other and are good indicators of species' vulnerability (Robinson & Redford 1986). Thus, we classified all species according to their trophic guild into herbivore, frugivore, carnivore, omnivore, insectivore, myrmecophage or piscivore according to Magioli et al. (2015). Additionally, we obtained adult body mass of each species from the literature (Emmons & Feer 1997, Paglia et al. 2012). We classified species, according to their dependence on forest and sensitivity to environmental disturbances, into: 1) hunted forest-dependent species, 2) non-hunted forest-dependent species, and 3) generalist species, based on the literature in addition to our knowledge (Emmons & Feer 1997, Souza et al. 2019, IUCN 2021). Specifically for xenarthrans, we used additional literature for their species classification (Ferreguetti et al. 2015, Attias et al. 2018, Rodrigues & Chiarello 2018; Appendix S3). Our classification might not be exclusive for some species, given that hunting pressure varies according to the ethnic group of hunters and the region. For example, both *Hydrochoerus hydrochaeris* and *Myocastor coypus* were classified as generalist species, yet we recognise that in some regions of the Atlantic Forest these species can be hunted. In these cases, we assume that hunting is infrequent or it is a non-game species, and therefore less vulnerable to impacts caused by hunting (see Cullen et al. 2001, Cardillo et al. 2005).

Data analyses

To assess the scale of effect of each spatial predictor (forest cover, edge density, number of patches, road density and human population density) on the overall species' occurrence pattern and occurrence data for each species, we adjusted Generalised Linear Models with binomial distribution, considering all buffer size radii (0.5, 1, 2, 4, and 6 km). For this, we performed single models relating species' occurrence data to each spatial predictor, separately for each buffer size. We selected the model with the lowest Akaike's Information Criterion value for each predictor, and then used the variable presented in the best model in further analyses. The scale of effect for the overall species' occurrence pattern varied between 500 m (for edge density and human population density), 1000 m (forest cover), 2000 m (number of patches) and 4000 m (road density), however, the scale of effect for each species varied widely between the variables analysed (see Appendix S5). After this procedure, we tested for multicollinearity among all explanatory variables used in the study, using Variance Inflation Factors. To do this, we considered the sampling effort as a fixed factor, as it can directly affect the detection probability. We did this procedure for all species combined and for each one individually, and excluded those presenting Variance Inflation Factor ≥ 3 (Dormann et al. 2013). In particular, we excluded forest cover for *Dasyprocta leporina*, number of patches for *Mazama americana* and road density for *Myocastor coypus*.

Given that the forest fragments were widely distributed throughout the entire Atlantic Forest biome and embedded within different landscape contexts, we first identified similar regions within the Atlantic forest. To do this, we followed a procedure similar to that used by Benchimol & Peres (2013) and Rios et al. (2021), where different layers were combined to spatially nest forest fragments in regions. The layers of major rivers of the Atlantic Forest and relief (IBGE 2017) were used as physical barriers to separate the regions. These regions often coincided with large blocks of forest or heavily forested areas that were identified using Google Earth Pro images. We plotted these layers in QGIS (version 3.4), and used them to define spatial clusters of fragments. At the end of this procedure, we obtained seven different regions and fragments were spatially nested within those regions.

We further performed Generalised Linear Mixed Models (GLMMs) with binomial distribution, containing all spatial predictors (patch size, forest cover, edge density, number of patches, road density and human population density) and species' life-history traits (trophic guild and body mass), to explain the patterns of occurrence of all species. First, we transformed patch size values in logarithm ($\log_{10}$) to homogenise the amplitude of the data and used the 'scale' function in R for all variables, due to differences in measurement units. In GLMMs, the sampling effort of each study was also included in the models as a fixed factor. The 'region', 'species' and 'fragment' were included as random factors. Then, we tested for spatial autocorrelation in the model residuals by applying Moran's I autocorrelation coefficient (range = -1 to 1) and semivariograms (Fortin & Dale 2005, Zuur et al. 2009). Finally, for each species, we considered only forest fragments in which the species might occur (i.e., was expected to occur or actually occurred), and adjusted GLMMs to relate variation in spatial variables (patch size, forest cover, edge density, number of patches, road density and human population density) to species' occurrence. We followed the same steps mentioned above, but using only 'region' as a random factor in the models, since we noted a variation among regions when observing the residual patterns. Whenever spatial autocorrelation was present, we accounted for it by performing GLMMs with penalised quasi-likelihood, with the glmmPQL function and included different autocorrelation structures (such as linear or spherical autocorrelation) according to the variogram's shape (Zuur et al. 2009). However, for *Dasyprocta leporina* we adjusted a Generalised Linear Model, controlling for spatial autocorrelation, due to the lack of convergence using GLMMs. We thus performed a simplification of this overall species' occurrence model by performing a stepwise procedure based on P-values (removing variables with $P > 0.05$) until all variables were significant ($P \leq 0.05$). We considered the model to be non-significant when the final model did not contain any significant explanatory variables. All analyses were performed in R 3.5.2. (R Core Team 2018) using the lme4 (Bates et al. 2015), MASS (Venables & Ripley 2002) and nlme (Pinheiro et al. 2020) packages.

RESULTS

We compiled mammal species' occurrence in forest fragments in nine Brazilian states. The highest number of forest fragments sampled were in the states of São Paulo (88 fragments) and Bahia (53). Considering all 220 forest fragments, only two retained a high percentage (>80%) of mammal species that were expected to occur, while 218 retained lower numbers of species, as follows: 18 sites: 60 - 80% of expected species, 32: 40 - 60%, 66: 20 - 40%, and 102: ≤20%. In total, eight mammal orders were recorded: Rodentia (6 species), Cingulata (5 species), Lagomorpha (1 species), Cetartiodactyla (5 species), Perissodactyla (1 species), Pilosa (2 species), Didelphimorphia (2 species) and Carnivora, with the latter comprising the most representaed order with 14 species. Each of the categories we used to classify species (i.e., hunted forest-dependent, non-hunted forest-dependent and generalist species) included 12 species. The most recorded species were *Dasypus novemcinctus* (*n*=173 forest fragments), *Nasua nasua* (*n*=142) and *Didelphis aurita* (*n*=112), whereas *Dasypus septemcinctus* (*n*=6), *Panthera onca* (*n*=7) and *Conepatus semistriatus* (*n*=8) presented the lowest number of records (Fig. 3).

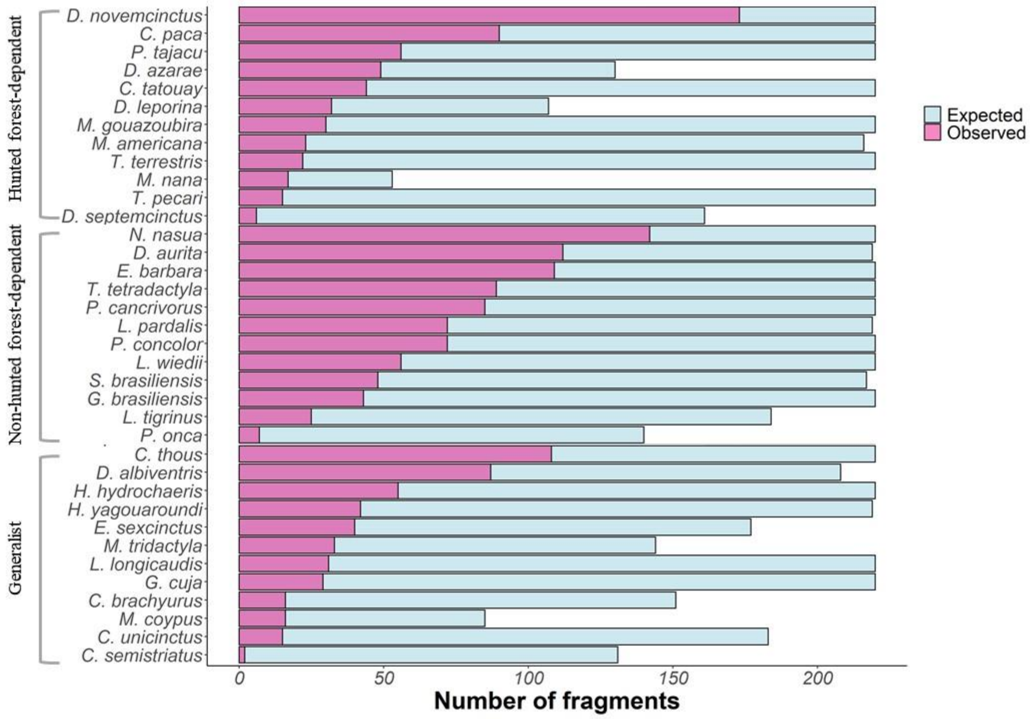


Fig. 3. Occurrence patterns of 36 mammal species recorded in 220 sampled forest fragments in the Brazilian Atlantic Forest. The coloured bars show the number of forest fragments where each species was expected and recorded.

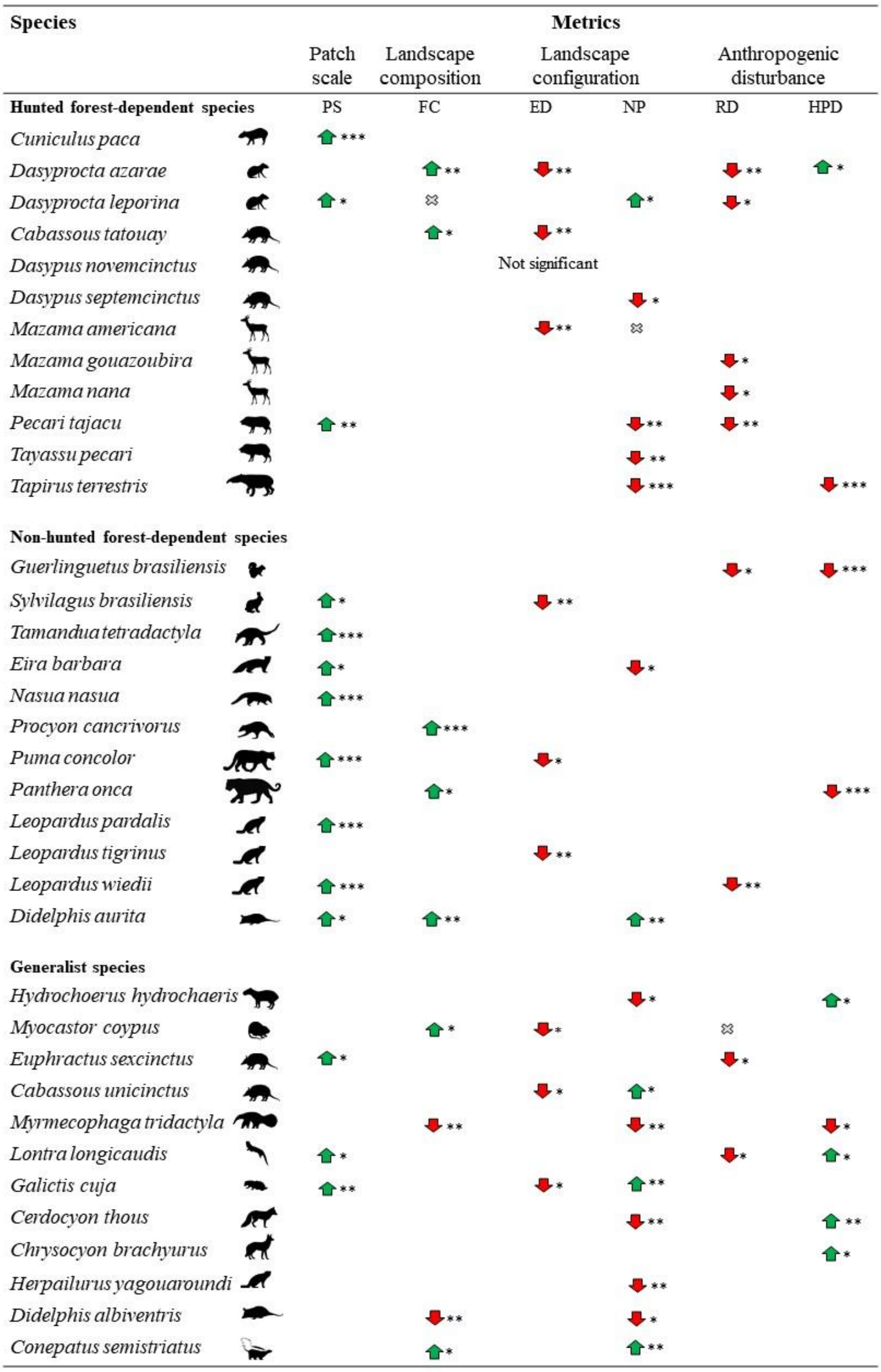
Effects of spatial predictors and species' life-history traits

When pooling all 36 species together, GLMMs revealed that landscapes containing large forest fragments, with low road density and with high human population density presented higher mammals species' occurrence, with large mammals being more likely to occur (Table 1).

Table 1. Best model explaining the relationship between patterns of occurrence of all 36 medium-sized and large mammal species and metrics (spatial predictors and life-history traits) in the 220 Atlantic Forest fragments included in our final database. The asterisks (*) indicate the level of significance of the variables (*** $P \leq 0.0001$, *$P \leq 0.05$).

Metrics	**β**	**Standard error**	***P*-value**
Patch size	0.7206	0.0880	2.73e-16***
Road density	-0.1741	0.0822	0.0342*
Human population density	0.1374	0.0710	0.0528*
Body mass	1.5011	0.6321	0.0175*

Although the model showed evidence of spatial autocorrelation, it was weak and probably did not change the reliability of the results. When assessing occurrence responses of each species individually, GLMMs showed that 13 of the 36 species were associated with a single predictor (Fig. 4). The species differed greatly in their responses, but patch size and number of patches were the main variables, relating to the occurrence of 14 and 15 species, respectively. Patch size, for instance, was positively associated with the occurrence of *Cuniculus paca*, *Puma concolor*, *Leopardus wiedii* and *Pecari tajacu*. Conversely, *Didelphis aurita* and *Nasua nasua* were less sensitive to path size, also occurring in small forest fragments (Fig. 5).



Species	Metrics					
	Patch scale	Landscape composition	Landscape configuration		Anthropogenic disturbance	
Hunted forest-dependent species	PS	FC	ED	NP	RD	HPD
Cuniculus paca	↑***					
Dasyprocta azarae		↑**	↓**		↓**	↑*
Dasyprocta leporina	↑*	✕		↑*	↓*	
Cabassous tatouay		↑*	↓**			
Dasypus novemcinctus			Not significant			
Dasypus septemcinctus				↓*		
Mazama americana			↓**	✕		
Mazama gouazoubira					↓*	
Mazama nana					↓*	
Pecari tajacu	↑**			↓**	↓**	
Tayassu pecari				↓**		
Tapirus terrestris				↓***		↓***
Non-hunted forest-dependent species						
Guerlinguetus brasiliensis					↓*	↓***
Sylvilagus brasiliensis	↑*		↓**			
Tamandua tetradactyla	↑***					
Eira barbara	↑*			↓*		
Nasua nasua	↑***					
Procyon cancrivorus		↑***				
Puma concolor	↑***		↓*			
Panthera onca		↑*				↓***
Leopardus pardalis	↑***					
Leopardus tigrinus			↓**			
Leopardus wiedii	↑***				↓**	
Didelphis aurita	↑*	↑**		↑**		
Generalist species						
Hydrochoerus hydrochaeris				↓*		↑*
Myocastor coypus		↑*	↓*		✕	
Euphractus sexcinctus	↑*				↓*	
Cabassous unicinctus			↓*	↑*		
Myrmecophaga tridactyla		↓**		↓**		↓*
Lontra longicaudis	↑*				↓*	↑*
Galictis cuja	↑**		↓*	↑**		
Cerdocyon thous				↓**		↑**
Chrysocyon brachyurus						↑*
Herpailurus yagouaroundi				↓**		
Didelphis albiventris		↓**		↓*		
Conepatus semistriatus		↑*		↑**		

Fig. 4. Best models explaining the relationship between each mammal species' occurrence and each spatial predictor: patch size (PS), forest cover (FC), edge density (ED), number of patches (NP), road density (RD) and human population density (HPD). The arrows indicate whether the effect was positive (upward pointing arrow) or negative (downward pointing arrow), asterisks (*) indicate the level of significance of the variables

(*** $P<0.0001$, ** $P<0.001$, * $P\leq0.05$) and 'x' indicates that the variable was not included in the model due to high collinearity (Variance Inflation Factor ≥3).

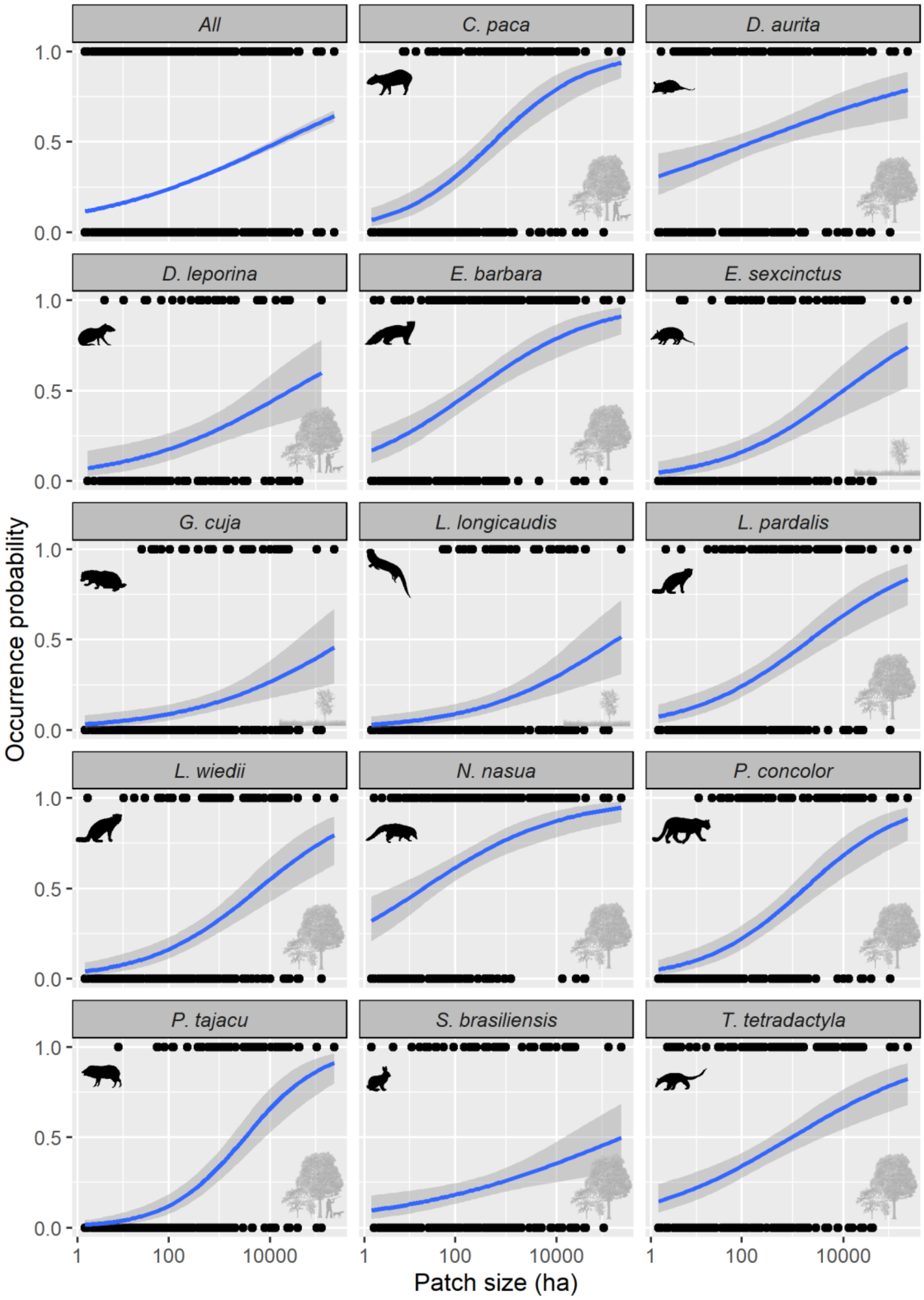


Fig. 5. Probability of occurrence of all 36 mammal species (All) and each medium-sized and large mammal species significantly affected by patch size.

The hunted forest-dependent species were mainly related to landscape configuration and anthropogenic disturbance variables. Landscape configuration was negatively related to the occurrence of seven species (Fig. 4). For example, *Mazama americana* (*β*=-0.861, *P*=0.002) was more likely to occur in landscapes with low edge density, while *Dasypus septemcinctus* (*β*=-1.897, *P*=0.017) and *Pecari tajacu* (*β*=-0.998, *P*=0.005) were more likely to occur in landscapes with low number of patches. The only exception was *Dasyprocta leporina* (*β*=1.000, *P*=0.049), which was positively associated by the number of patches. Road density was negatively related to the occurrence of *Mazama gouazoubira* (*β*=-0.412, *P*=0.029) and *Mazama nana* (*β*=-0.929, *P*=0.015), while human population density was positively related to the occurrence of *Dasyprocta azarae* (*β*=100.687, *P*=0.040) and negatively related to the occurrence of *Tapirus terrestris* (*β*=-6.009, *P*<0.001).

Non-hunted forest-dependent species were mainly related to patch size, which positively influenced the occurrence of eight of the 12 species. In fact, the occurrence of *Tamandua tetradactyla* (*β*=0.792, *P*<0.001), *Nasua nasua* (*β*=0.688, *P*<0.001) and *Leopardus pardalis* (*β*=1.292, *P*<0.001) was exclusively explained by patch size. Landscape configuration variables were also important in explaining the occurrence of eight species. For example, *Sylvilagus brasiliensis* (*β*=-15.243, *P*=0.003), *Puma concolor* (*β*=-2.621, *P*=0.042) and *Leopardus tigrinus* (*β*=-6.465, *P*=0.003) were negatively related by edge density, while *Eira barbara* (*β*=-0.459, *P*=0.035) and *Didelphis aurita* (*β*=0.764, *P*=0.007) were negatively and positively associated to the number of patches, respectively.

Finally, the occurrence of generalist species could be predicted mainly by landscape configuration and anthropogenic disturbances, influencing the occurrence of nine and six species, respectively. While edge density had a predominantly negative relation on

Myocastor coypus (*β*=-31.286, *P*=0.018), *Cabassous unicinctus* (*β*=-0.914, *P*=0.038) and *Galictis cuja* (*β*=-0.661, *P*=0.042), the number of patches showed negative relation for *Hydrochoerus hydrochaeris* (*β*=-0.494, *P*=0.025), *Myrmecophaga tridactyla* (*β*=-0.906, *P*=0.006), *Cerdocyon thous* (*β*=-0.604 *P*=0.002), *Herpailurus yagouaroundi* (*β*=-0.791, *P*=0.004) and *Didelphis albiventris* (*β*=-0.177, *P*=0.022), in addition to positive relation for *Cabassous unicinctus* (*β*=0.699, *P*=0.039), *Galictis cuja* (*β*=0.684, *P*=0.001) and *Conepatus semistriatus* (*β*=1.584, *P*=0.016). Similarly, road density also had a predominantly negative relation for *Euphractus sexcinctus* (*β*=-16.577, *P*=0.037) and *Lontra londicaudis* (*β*=-0.668, *P*=0.024). Human population density was positively associated with occurrence of *Hydrochoerus hydrochaeris* (*β*=0.651, *P*=0.031), *Lontra londicaudis* (*β*=1.505, *P*=0.026), *Cerdocyon thous* (*β*=2.975, *P*=0.008) and *Chrysocyon brachyurus* (*β*=1.239, *P*=0.037) and negatively associated with occurrence of *Myrmecophaga tridactyla* (*β*=-7.287, *P*=0.053; Fig. 4, Appendix S6).

DISCUSSION

As far as we are aware, this is the first study to assess the influence of spatial predictors on the occurrence patterns of medium-sized to large terrestrial mammal species within the threatened Brazilian Atlantic Forest. By compiling data from 220 forest fragments varying in size and landscape contexts, we revealed that most species have been extirpated from their original areas of occurrence. Yet the key factors predictive of species' occurrence vary greatly among the species we surveyed, and are determined considerably by spatial predictors. In particular, patch size appeared as a powerful predictor, positively influencing 42% of all mammal species – mostly forest-dependent but non-hunted species. Conversely, the occurrence of hunted and forest-dependent species was mainly predicted by landscape configuration and anthropogenic stressors.

Given the long history of deforestation and hunting in this global biodiversity hotspot (Canale et al. 2012, Bogoni et al. 2018), which has already led to largely defaunated forest fragments, we highlight which mammal species have been mostly extirpated in HMLs and how policy stakeholders can prevent the further collapse of mammal assemblages through a landscape perspective.

Predictors of overall species' occurrence

The occurrence of the overall mammal species in forest fragments was strongly related to patch size, anthropogenic disturbances and body mass. These results partially confirm our predictions, as we initially expected stronger influence of forest cover as previously observed for patterns of mammal species richness in the Atlantic Forest (see Rios et al. 2021). This shows that, for Atlantic Forest mammals, greater occupancy is observed within large forest fragments surrounded by lower road density and exhibiting higher human density, including species showing greater body mass. Previous studies also found that patch size and anthropogenic disturbances were important predictors, explaining mammal' occurrence patterns (Urquiza-Haas et al. 2009, Benchimol & Peres 2015), richness (Michalski & Peres 2007), population density (Michalski & Peres 2007, Tucker et al. 2020) and mortality rates (Caceres 2011). However, we would like to highlight that the high probability of mammal occurrence in areas that are densely populated by humans found here must be interpreted with caution. We suggest that this positive association of human population density is due to a high probability of occurrence of generalist species in these densely populated areas, while forest-dependent species are unlikely to occur in these areas.

Spatial predictors of the occurrence of mammal groups

Contrary to our predictions, landscape composition did not prevail over landscape configuration in explaining forest-dependent mammal occurrence. For instance, forest cover was a weak predictor of the occurrence of hunted forest-dependent species. The opposite pattern was found for mammal richness (Rios et al. 2021), where the effects of landscape composition were prevalent, indicating that the pattern may differ according to the response variable. On the other hand, we found strong negative relation of landscape configuration, road density and human population, with 83% of hunted forest-dependent species being related by at least one of these variables. Increasing edge density and number of patches negatively influenced eight of the 12 species we assessed within the category, indicating that mammal species' occurrence was related to the spatial configuration of the remaining forest. This predominant negative relationship of landscape configuration on species' occurrence may be due to the increased edge effect and the contrasting matrix that surrounds most of these forest fragments. The forest fragments studied here were immersed mainly in a matrix of agriculture and pasture, which may intensify negative edge effects (Harper et al. 2005), in addition to representing a less permeable matrix, therefore reducing connectivity among fragments (Watling et al. 2011). This reinforces the need to keep forest fragments embedded within high-quality matrices, which would enhance the likelihood of these forest-dependent species occurring in the Atlantic Forest (Arroyo-Rodríguez et al. 2020). Additionally, our results on species' occurrence do not corroborate with the expectation that fragmentation has weak and, when significant, predominantly positive effects (Fahrig 2003, 2017). Our findings are similar to those of another study on the occupancy of medium-sized and large mammals in forest fragments in Guatemala (Thornton et al. 2011); both studies indicate that landscape configuration should be taken into account when developing conservation strategies for mammals.

The negative association of hunted forest-dependent species to anthropogenic disturbances was an expected pattern. The presence of roads and human population has been widely used as a predictor of species' vulnerability to extinction and hunting (Peres 2000, Benítez-López et al. 2010, Lima et al. 2020). The negative relation of road density on hunted forest-dependent species reinforce the widely recognised and damaging effects of roads on mammals, since highways can facilitate human access to fragments, increase mortality due to collisions, or act as barriers to species' movements (Benítez-López et al. 2010, Caceres 2011, Espinosa et al. 2014). In addition, hunting can be a determining factor for mammal persistence. For example, although many large mammal species are associated with more forested landscapes, their populations can become extinct or drastically reduced in forested areas due to hunting, as has been observed for large mammal species in landscapes of the Brazilian Amazon (Sampaio et al. 2010). Surprisingly, we did not find a strong relationship between human population density and the occurrence of hunted forest-dependent species, except for *Tapirus terrestris*. However, we highlight that the negative relationship between human population density and the occurrence of this species was mainly apparent at a small spatial scale, with a 0.5 km radius. This information could inform decisions of policy-makers designing conservation strategies aimed at reducing the negative impact of the human population on *Tapirus terrestris* in HLMs.

Non-hunted forest species were strongly related to patch size. In particular, our results revealed that patch size was the most important predictor for this category, and more than 65% of non-hunted forest-dependent species were more likely to occur in larger forest fragments than in smaller ones. In fact, patch size has been recognised as a powerful predictor of patterns of occurrence of medium-sized and large mammal species in Neotropical forests (Michalski & Peres 2005, Garmendia et al. 2013, Jorge et al. 2013). These larger forest fragments can also have high structural vegetation complexity and therefore higher habitat quality, which has already been shown to be important for arboreal mammals (Cudney-Valenzuela et al. 2021). In addition, several species have large family group sizes, such as *Nasua nasua* that forms groups of about 30 individuals (Emmons & Feer 1997), and large groups may require large areas of habitat to persist. Considering that ~80% of Atlantic Forest fragments are <50 ha and fewer than 0.03% are >10000 ha (Ribeiro et al. 2009), our results clearly demonstrate that non-hunted forest-dependent mammal species have been severely extirpated in HLMs due to the shrinkage in fragment size, with potential negative impacts for ecosystem functioning in those severely defaunated fragments.

Finally, our findings highlight the importance of configuration and anthropogenic disturbance as key predictors of mammal occurrence for those species that are more resilient to disturbances. We found a wide variation in results to spatial predictor metrics for generalist species. With the exception of *Cabassous unicinctus*, *Galictis cuja* and *Conepatus semistriatus*, which were more likely to occur in landscapes with greater numbers of patches, the other species were negatively related by configuration variables. This shows that even species presenting more generalist habits and with greater tolerance to disturbances can be sensitive to landscape modification. Thus, landscapes containing high edge density and greater numbers of patches are less suitable for generalist species. On the other hand, road density negatively influenced two species (i.e., *Euphractus sexcinctus* and *Lontra longicaudis*), reinforcing the documented widespread negative effects of roads for mammals (Espinosa et al. 2014). However, as expected, sites with high human population density were important for safeguarding some species, including

Hydrochoerus hydrochaeris, *Lontra longicaudis*, *Cerdocyon thous* and *Chrysocyon brachyurus*. These species consume a wide range of resources and are able to explore disturbed areas (Reis et al. 2006, Vynne et al. 2014), which may explain their greater occurrence in fragments surrounded by areas with high human population density.

‘Winner’ and ‘loser’ mammal species

We unveiled a non-random pattern of mammal species’ occurrence in the Atlantic Forest: some species are able to adapt to changes and persist, while others are at serious risk of local extirpation in the near future. In fact, some mammal species included here have a high probability of thriving in HMLs: the ‘winner’ species. Species benefiting from areas close to humans, including *Hydrochoerus hydrochaeris*, *Cerdocyon thous* and *Chrysocyon brachyurus*, can be classified as ‘winner’ species across the biome. On the other hand, most species exhibited greater sensitivity to habitat changes, occurring in a small number of forest fragments and demonstrating high chances of becoming locally extirpated: the ‘loser’ species. These include *Dasyprocta leporina*, *Euphractus sexcinctus*, *Galictis cuja*, *Lontra longicaudis*, *Leopardus wiedii*, *Pecari tajacu* and *Sylvilagus brasiliensis*, which were unable to reach a 20% probability of occurrence in small forest fragments of 50 ha. However, it is worth noting that there are possible limitations due to the minimum sampling effort used in our study (30 camera/day or 730 hours; see Tobler et al. 2008, Si et al. 2014). This threshold may have affected the probability of pseudo-absences, mainly of rare or scansoral species, which would require greater sampling effort to be recorded.

We also revealed that while 83% of the Atlantic Forest is composed of small forest fragments ≤ 50 ha (Ribeiro et al. 2009), no species related by patch size reached a 60% probability of occurrence in forest fragments of this size. Specifically, *Dasyprocta leporina* and *Euphractus sexcinctus* require forest fragments >100 ha to achieve a 60%

chance of occurrence, while *Leopardus wiedii*, *Leopardus pardalis*, *Puma concolor*, *Pecari tajacu* and *Tamandua tetradactyla* require large forest fragments between 10000 - 35000 ha, which represents only about 0.03% of the remaining forest fragments in the entire biome (Ribeiro et al. 2009). Clearly, these species need more attention, as the current deforestation of the Atlantic Forest severely threatens the persistence of these species in the long term. Other studies corroborate our findings (Jorge et al. 2013, Magioli et al. 2021), highlighting the urgent need to conserve the remaining large forest fragments and prioritise restoration programs. In addition, species of the genus *Dasyprocta*, *Mazama* and other game species such as *Pecari tajacu* showed high sensitivity to high road density in the landscape. This indicates greater susceptibility to anthropogenic pressures such as hunting, which, although legally prohibited, is widespread in the biome (Cullen et al. 2001, Castilho et al. 2017). We finally highlight that several species currently not classified as threatened with extinction (Critically Endangered, Endangered, or Vulnerable) according to the international assessment (IUCN 2021) or not included in the national threatened species list (Portaria n. 444 MMA 2014) are indeed ‘loser’ species in the Atlantic Forest, including *Dasyprocta leporina*, *Leopardus pardalis*, *Puma concolor*, *Pecari tajacu* and *Tamandua tetradactyla*. Our results therefore reveal their greater susceptibility to becoming locally extinct in the biome, indicating the urgency of conservation efforts as a preventative measure to ensure their long-term persistence.

CONCLUSIONS

Identifying which factors drive species to extinction is an urgent step towards predicting mammal occurrence in HLMs, especially in threatened biomes such as the Atlantic Forest. We observed strong associations of patch size, anthropogenic disturbances and body mass with overall patterns of mammal occurrence. Yet, the contrasting species’ responses indicate that habitat specialisation and vulnerability to hunting greatly explain the sensitivity of species to patch and/or landscape changes. Our results support the idea that it is necessary to design conservation strategies that not only take into account the mitigation of forest loss, but also incorporate measures to reduce habitat fragmentation, edge effects and road density effects on mammals in the Atlantic Forest. Thus, it is essential to maintain large forest tracts to guarantee the long-term occurrence of most species. However, keeping these sites under legal protection is also fundamental; only 9.3% of forest fragments are currently legally protected in the Atlantic Forest (Ribeiro et al. 2009). Although these sites are still subject to human pressures, they are essential for safeguarding biodiversity (De Carvalho & Morato 2013, Castilho et al. 2017). Furthermore, attenuating the contrast between the forest and the surrounding matrix and mitigating the effects of roads must be priority actions. As the most important management actions, we expressly recommend: 1) the implementation of restoration programs, to increase forest fragment size within HLMs; 2) the enforcement of hunting restrictions in both protected areas and private landholdings, to prevent hunted forest-dependent species from rapidly becoming extinct either at the landscape scale or at the biome scale; 3) the reintroduction of the vanished mammal fauna into their natural habitats, to bring back the most vulnerable species (‘loser’ species), such as the charismatic *Leopardus pardalis*, *Puma concolor*, *Panthera onca*, *Pecari tajacu* and *Tamandua tetradactyla,* and consequently enable the provision of key ecosystem services they provide (Bogoni et al. 2020, Magioli et al. 2021). These measures are even more relevant in the current risky scenario in which Brazil finds itself, where environmental policies are being dismantled and weakened by the Brazilian government, making the future of the Atlantic Forest and mammals uncertain (Barbosa et al. 2021).

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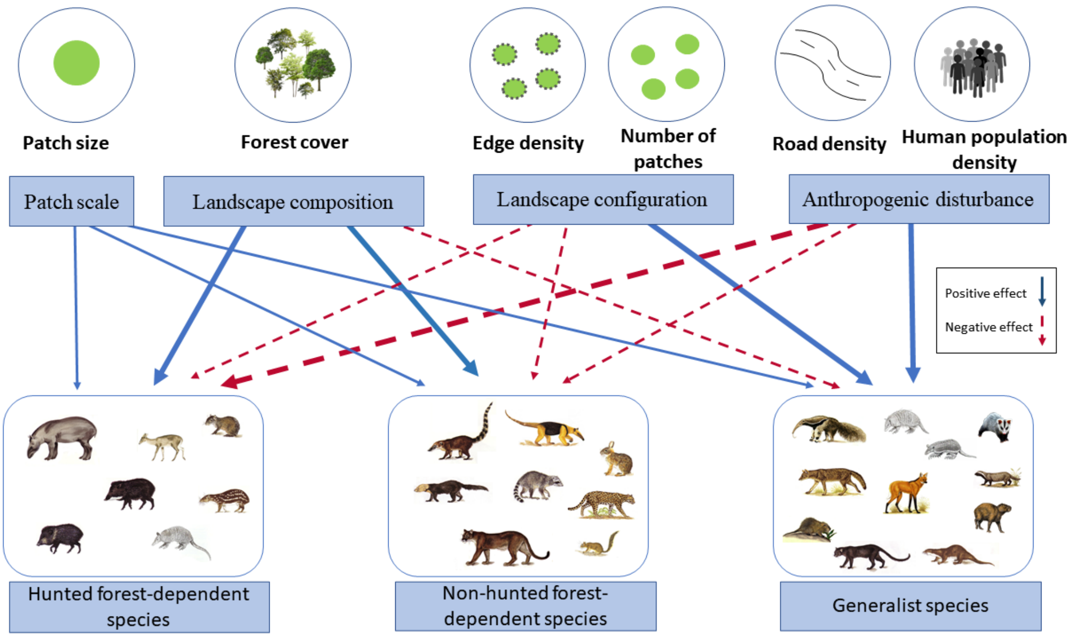
GRAPHICAL ABSTRACT



The thickness of the arrow indicates whether the effect is strong or weak

Mammal species respond in different ways to changes in their habitat. To find out which are the main predictors of medium-sized and large mammal occurrence in the Atlantic Forest, we gathered information on 36 species that show differences in their dependence on forests and sensitivity to environmental disturbances. We depicted the relation (positive or negative) of each predictor variable on the occurrence of mammal species. The thickness of the arrow indicates the magnitude of the effects. Hunted forest-dependent species are more likely to occur in landscapes with low edge density and number of patches and low road density, while non-hunted forest-dependent species have a high probability of occurring in large forest fragments. On the other hand, we found that generalist species are more likely to occur in landscapes with low edge density and number of patches, but are more prevalent in landscapes with high human population density. Conservation efforts should prioritize actions that reduce forest loss but also take into account the landscape configuration and mitigate the effects of road density to maintain high species occurrence.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s website.

Appendix S1. Predictions for the mammal species’ occurrence

Appendix S2. List of the studies used in the research.

Appendix S3. Information on mammal species

Appendix S4. Description of variables

Appendix S5. Scale of effect

Appendix S6. Parameters for the best models

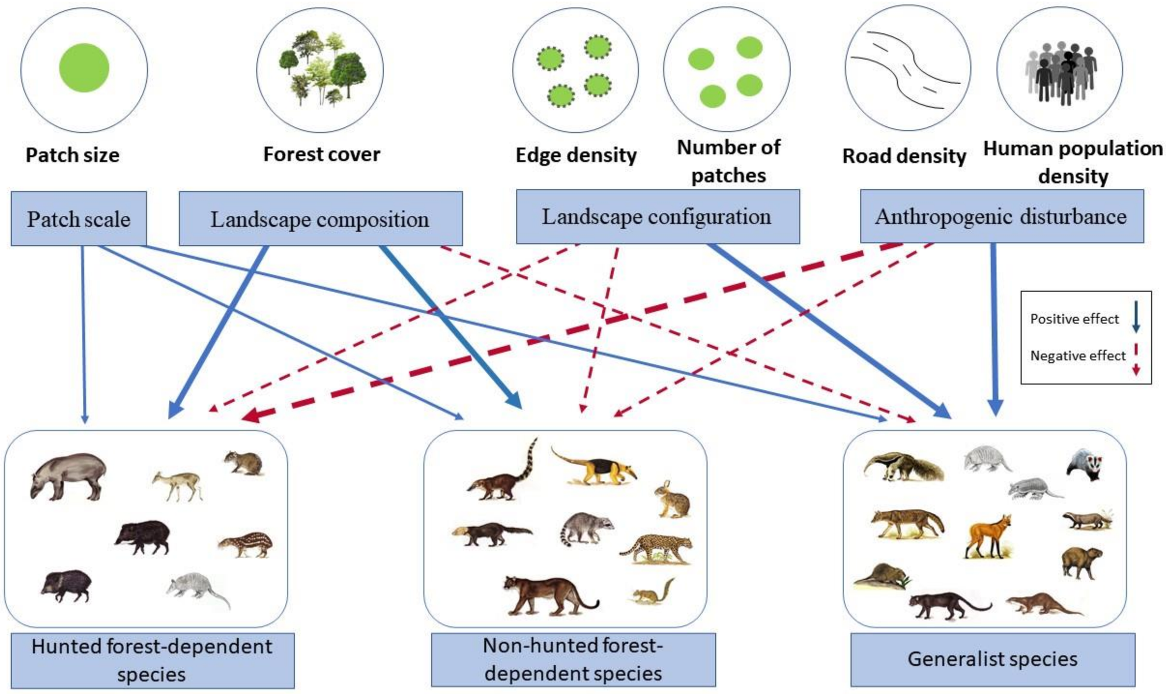
Mammal Review

Supplementary Material

Spatial predictors and species' traits: evaluating what really matters for medium-sized and large mammals in the Atlantic Forest, Brazil

Appendix S1. Predictions for the mammal species' occurrence

Appendix S1. Predictions for the mammal species' occurrence in relation to spatial variables herein assessed, based on different habitat-specialization and hunting pressure groups.



The thickness of the arrow indicates whether the effect is strong or weak

Appendix S2. List of the studies used in the research.

Appendix S2. Supplementary Literature Cited – List of the studies used in the research. The studies were obtained from the “ATLANTIC-CAMTRAPS” datapaper” (Lima et al. 2017), ATLANTIC MAMMALS” (Souza et al. 2019) and from the Scopus and Google Scholar databases. We also included three unpublished datasets - our own data and provided by researchers (Magioli & Morato and Flesher).

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Appendix S3. Information on mammal species

Appendix S3. Information on each 36 species of medium-sized and large mammals recorded in forest fragments throughout the Atlantic Forest. Information on body mass were extracted from Paglia et al. (2012), trophic guide (HB = herbivore, Fr = frugivore, On = omnivore, Gr = granivore, In = insectivore, Myr = myrmecophago, Ps = psivivore, Ca = carnivore) were extracted from Magioli et al. (2015), and species sensitivity (HFD = hunted forest-dependent and NFD = non-hunted forest-dependent and GEN=Generalist) were based on published literature (see Emmons & Feer (1997), IUCN (2020), Souza et al. (2019), Ferreguetti et al. (2015), Attias et al. (2018), Rodrigues & Chiarello (2018)) in addition to our own knowledge. Threat category according to IUCN red list (LC = Least Concern, DD = Data Deficient, EN = Endangered, VU = Vulnerable and NT = Near Threatened), and the national list of threatened species according to the Portaria MMA n. 444 (2014).

Taxon	**Common name**	**Body mass (Kg)**	**Trophic guild**	**Sensitivity**	**Threat Category**	
					IUCN	Brazilian list
Rodentia						
Caviidae						
Hydrochoerus hydrochaeris (Linnaeus, 1766)	Capybara	35-65	Hb	GEN	LC	-
Cuniculidae						
Cuniculus paca (Linnaeus, 1766)	Agouti	9.3	Fr/Hb	HFD	LC	-
Myocastoridae						
Myocastor coypus (Molina, 1782)	Coypu	1-1.08	Fr/On	GEN	LC	-
Dasyproctidae						
Dasyprocta azarae (Lichtenstein, 1823)		2.3-3.5	Fr/Gr	HFD	DD	-

Dasyprocta leporina (Linnaeus, 1758)	Red-rumped Agouti	3-8	Fr/Gr	HFD	LC	-
Sciuridae						
Guerlinguetus brasiliensis (Gmelin, 1788)	Squirrel	0.8	Fr/On	NFD	-	-
Cingulata						
Dasypodidae						
Dasypus novemcinctus (Linnaeus, 1758)	Nine-banded Armadillo	3.65	In/On	HFD	LC	-
Dasypus septemcinctus (Linnaeus, 1758)	Brazilian Lesser Long-nosed Armadillo	1.5	In/On	HFD	LC	-
Chlamyphoridae						
Euphractus sexcinctus (Linnaeus, 1758)	Yellow Armadillo	5.4	In/On	GEN	LC	-
Cabassous tatouay (Desmarest, 1804)	Greater Naked-tailed Armadillo	5.35	Myr	HFD	LC	-
Cabassous unicinctus (Linnaeus, 1758)	Southern Naked-Tailed Armadillo	3.2	Myr	GEN	LC	-
Lagomorpha						
Leporidae						
Sylvilagus brasiliensis (Linnaeus, 1758)	Tapeti	1.2	Hb	NFD	EN	-
Cetartiodactyla						
Cervidae						
Mazama americana (Erxleben, 1777)	Red Brocket	24-48	Fr/Hb	HFD	DD	-
Mazama gouazoubira (G. Fischer, 1814)	Gray Brocket	17-25	Fr/Hb	HFD	LC	-
Mazama nana (Hensel, 1872)	Brazilian Dwarf Brocket	15-20	Fr/Hb	HFD	VU	VU
Tayassuidae						
Pecari tajacu (Linnaeus, 1758)	Collared Peccary	17-35	Fr/Hb	HFD	LC	-
Tayassu pecari (Link, 1795)	White-lipped Peccary	25-45	Fr/Hb	HFD	VU	VU
Perissodactyla						
Tapiridae						

Tapirus terrestris (Linnaeus, 1758)	Lowland Tapir	260	Fr/Hb	HFD	VU	VU
Pilosa						
Myrmecophagidae						
Myrmecophaga tridactyla (Linnaeus, 1758)	Giant Anteater	30.5	Myr	GEN	VU	VU
Tamandua tetradactyla (Linnaeus, 1758)	Southern Tamandua	5.2	Myr	NFD	LC	-
Carnivora						
Mustelidae						
Lontra longicaudis (Olfers, 1818)	Neotropical Otter	6	Ps	GEN	NT	-
Eira barbara (Linnaeus, 1758)	Tayra	4-10	Ca	NFD	LC	-
Galictis cuja (Molina, 1782)	Lesser Grison	1-3	Ca	GEN	LC	-
Procyonidae						
Nasua nasua (Linnaeus, 1766)	South American Coati	5.1	Fr/On	NFD	LC	-
Procyon cancrivorus (G. Cuvier, 1798)	Crab-eating Raccoon	5.4	Fr/On	NFD	LC	-
Canidae						
Cerdocyon thous (Linnaeus, 1766)	Crab-eating Fox	6.5	In/On	GEN	LC	-
Chrysocyon brachyurus (Illiger, 1815)	Maned Wolf	25	Ca/On	GEN	NT	VU
Felidae						
Puma concolor (Linnaeus, 1771)	Puma	22-70	Ca	NFD	LC	VU
Panthera onca (Linnaeus, 1758)	Jaguar	61-158	Ca	NFD	NT	VU
Herpailurus yagouaroundi (É. Geoffroy, 1803)	Jaguarundi	3-6	Ca	GEN	LC	VU
Leopardus pardalis (Linnaeus, 1758)	Ocelot	11	Ca	NFD	LC	-
Leopardus tigrinus (Schreber, 1775)	Northern Tiger Cat	1.5-3	Ca	NFD	VU	EN
Leopardus wiedii (Schinz, 1821)	Margay	3-9	Ca	NFD	NT	VU
Conepatus semistriatus (Boddaert, 1785)	Striped Hog-nosed Skunk	2.4	In/On	GEN	LC	-
Didelphimorphia						
Didelphidae						

Didelphis aurita (Wied-Neuwied, 1826)	Brazilian Common Opossum	0.67-1.8	Fr/On	NFD	LC	-
Didelphis albiventris (Lund, 1840)	White-eared Opossum	0.5-2.7	Fr/On	GEN	LC	-

Appendix S4. Description of variables

Appendix S4 - Description of each spatial variable calculated for the 220 forest fragments of the Atlantic Forest included in our database. The metrics values on the landscape scale refer to the 2 km buffer. The buffers of other sizes resulted in different values for these variables.

Variables (Code)	**Description**	**Unit**	**Range (mean ± SD)**
Patch size	Total area of forest fragment	ha	5200.51 ± 17549.99
Landscape composition			
Forest cover	Percentage of primary and secondary forests within the landscape	%	0.49 ± 0.33
Landscape configuration			
Edge density	Total perimeter of all forest fragments divided by landscape size	meters/m^2	44.78 ± 134.04
Number of patches	Total number of forest fragments within of the landscape	-	18.95 ± 15.04
Anthropogenic disturbance			
Road density	Total length of roads divided by the size of the landscape	meters/m^2	0.003 ± 0.0008
Human population density	Total number of humans divided by landscape size	ind/m^2	43.38 ± 268.15

Appendix S5. Scale of effect

Appendix S5 – Scale of effect selected (in meters) for each landscape variable used in this study. FC = Forest Cover, ED = Edge Density, NP = Number of patches, RD = Road Density, HPD = Human Population Density.

Species	Landscape composition	Landscape configuration		Anthropogenic disturbance	
	FC	ED	NP	RD	HPD
Hunted forest-dependent species					
Cuniculus paca	1000	1000	2000	4000	1000
Dasyprocta azarae	500	6000	6000	6000	500
Dasyprocta leporina	2000	500	2000	2000	1000
Cabassous tatouay	1000	1000	1000	4000	1000
Dasypus novemcinctus	6000	6000	2000	500	2000
Dasypus septemcinctus	4000	2000	4000	500	1000
Mazama americana	1000	4000	4000	1000	1000
Mazama gouazoubira	2000	6000	6000	4000	500
Mazama nana	500	6000	500	6000	4000
Pecari tajacu	2000	2000	2000	4000	6000
Tayassu pecari	4000	2000	6000	4000	1000
Tapirus terrestris	1000	1000	6000	4000	500
Non-hunted forest-dependent species					
Guerlinguetus brasiliensis	1000	500	1000	6000	500
Sylvilagus brasiliensis	6000	6000	2000	1000	4000
Tamandua tetradactyla	1000	500	6000	2000	2000
Eira barbara	2000	500	2000	4000	4000
Nasua nasua	1000	6000	1000	6000	2000
Procyon cancrivorus	1000	6000	1000	4000	500
Puma concolor	500	2000	4000	4000	500
Panthera onca	6000	1000	6000	6000	500
Leopardus pardalis	1000	2000	2000	2000	500
Leopardus tigrinus	2000	2000	1000	1000	500
Leopardus wiedii	1000	2000	2000	6000	6000
Didelphis aurita	4000	500	6000	1000	500
Generalist species					
Hydrochoerus hydrochaeris	500	6000	4000	4000	4000
Myocastor coypus	1000	6000	2000	500	4000
Euphractus sexcinctus	1000	500	1000	6000	2000
Cabassous unicinctus	2000	2000	500	6000	6000
Myrmecophaga tridactyla	6000	6000	6000	500	6000

Lontra longicaudis	500	500	1000	4000	6000
Galictis cuja	1000	500	1000	6000	500
Cerdocyon thous	1000	500	2000	4000	6000
Chrysocyon brachyurus	500	6000	1000	1000	6000
Herpailurus yagouaroundi	500	6000	1000	6000	1000
Didelphis albiventris	6000	6000	500	6000	2000
Conepatus semistriatus	1000	6000	6000	4000	2000

Appendix S6. Parameters for the best models

Appendix S6 – Parameters (β ± Std.Error) of the best model explaining the relationship between each mammal species’ occurrence and spatial predictors. The significant coefficients are represented by asterisks (*$P \leq 0.05$, **$P < 0.01$ and ***$P < 0.001$). 1 +- 5

Species	**Patch size**	**Forest cover**	**Edge density**	**Number of patches**	**Road density**	**Human population density**	**Random effects**			
	β ± Std.Error	β ± Std.Error	β ± Std.Error	β ± Std.Error	β ± Std.Error	β ± Std.Error	Intercept	Residual	Variance	Std.Dev.
Hunted forest-dependent species										
C. paca	1.073 ± 0.205***						0.960	0.937		
D. azarae		0.760 ± 0.271**	-25.009 ± 7.259**		-41.736 ± 12.703**	100.687 ± 0.040*			0	0
D. leporina	0.856 ± 0.424*	Excluded		1.000 ± 0.508*	-2.786 ± 1.338*		-	-	-	-
C. tatouay		0.539 ± 0.266*	-2.010 ± 0.741**						0.033	0.183
D. novemcinctus			Not significant						0.469	0.685
D. septemcinctus				-1.897 ± 0.800*					0	0
M. americana			-0.861 ± 0.276**	Excluded			0.000	0.885		
M. gouazoubira					-0.412 ± 0.187*		0.769	0.911		
M. nana					-0.929 ± 0.381*				0.234	0.484
P.tajacu	0.730 ± 0.275**			-0.998 ± 0.354**	-0.631 ± 0.236**				0	0
T. pecari				-2.241 ±					1.598	1.264

				0.772**						
T. terrestris				-3.455 ± 0.992***		-6.009 ± 44.390***			4.573	2.139
Non-hunted forest-dependent species										
G. brasiliensis					-17.458 ± 7.276*	-1422.633 ± 357.225***			1.805	1.343
S. brasiliensis	0.331 ± 0.174*		-15.243 ± 5.005**				0.968	0.896		
T. tetradactyla	0.792 ± 0.181***								0.186	0.432
E. barbara	0.490 ± 0.216*			-0.459 ± 0.216*			0.357	1.000		
N. nasua	0.688 ± 0.186***						0.357	1.004		
P. cancrivorus		0.943 ± 0.228***							0.705	0.839
P. concolor	0.823 ± 0.202***		-2.621 ± 1.279*				0.366	0.940		
P. onca		9.187e-01 ± 4.775e-01*				-6.896e+05 ± 1.709e+01***			5.073e-29	7.123e-15
L.pardalis	1.292 ± 0.242***						1.526	0.923		
L. tigrinus			-6.465 ± 2.176**						0.257	0.507
L. wiedii	0.697 ± 0.215***				-20.743 ± 6.813**		0.679	0.953		
D. aurita	0.446 ± 0.208*	0.923 ± 0.332**		0.764 ± 0.281**			0.590	0.968		
Generalist species										
H.hydrochaeris				-0.494 ± 0.219*	Excluded	0.651 ± 0.299*	0.637	0.930		
M. coypus		0.695 ± 0.316*	-31.286 ± 13.230*						0	0
E. sexcinctus	0.561 ±				-16.577 ±		2.427446e-09	0.974		

	0.238*				7.901*					
C.unicinctus			-0.914 ± 0.440*	0.699 ± 0.339*					0.350	0.591
M. tridactyla		-0.833 ± 0.269**		-0.906 ± 0.326**		-7.287 ± 3.737*	0.001	0.909		
L. longicaudis	0.594 ± 0.273*				-0.668 ± 0.295*	1.505 ± 0.675*			0.952	0.976
G. cuja	0.635 ± 0.201**		-0.661 ± 0.323*	0.684 ± 0.207**			1.084	0.848		
C. thous				-0.604 ± 0.198**		2.975 ± 1.108**	0.869	0.962		
C. brachyurus						1.239 ± 0.595*			0.029	0.170
H. yagouaroundi				-0.791 ± 0.278**					0.919	0.959
D. albiventris		-0.795 ± 0.248**		-0.177 ± 0.077*			0.000	0.959		
C. semistriatus		1.773 ± 0.739*		1.584 ± 0.553**					0	0

CAPÍTULO III

LINKING LANDSCAPE FEATURES, ANTHROPOGENIC STRESSORS AND MAMMAL ABUNDANCE TO UNVEIL SEED REMOVAL PATTERNS IN TROPICAL DEFORESTED LANDSCAPES

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Linking landscape features, anthropogenic stressors and mammal abundance to unveil seed removal patterns in tropical deforested landscapes

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Abstract

Land use changes and related anthropogenic pressures are responsible for biodiversity declines and threaten the provision of ecosystem services. Seed dispersal is a key ecological process, thus, understanding the factors that can limit this process in human-modified landscapes is essential to ensure ecosystem functioning. Using structural equation models, we evaluated the direct and indirect effects of habitat amount, landscape configuration, anthropogenic stressors and abundance of potentially seed disperser mammals on seed removal patterns of *Eschweilera ovata* (Lecythidaceae) in 18 Atlantic Forest fragments in the southern region of Bahia, Brazil. We used camera traps to record potentially seed dispersal mammals and spool line experiment to assess the ultimate fate of the seeds. We reveal a direct effect of landscape-scale forest cover on the percentage of seeds removed, in which seed removal decrease in more forested landscapes. We also found a negative effect of human population density on mammal abundance. We suggest that the mechanisms that explain seed removal in human-modified landscapes can often be complex and that additional factors may help to explain seed removal patterns in human modified landscapes. To reduce the impacts of human population on mammals, we recommend implementing Environmental Education programs and developing alternatives to increase local income, especially in the communities surrounding the forest fragments studied. Moreover, it is essential the supervision and enforcement of environmental laws.

Keywords: Atlantic forest; habitat amount; landscape configuration; mammal disperser; seed dispersal; seed predation.

1. Introduction

Global biodiversity is facing fast rates of decline mainly due to changes in land use and related anthropogenic pressures (Dirzo et al., 2014; Newbold et al., 2015; 2020). In tropical regions, land use changes are more intense, and the negative effects of these disturbances on biodiversity are even more pronounced (Gibbs et al., 2010; Gibson et al., 2011). This results not only in the decay of species richness, but also change species composition, leading to the loss of ecological functions and provision of relevant ecosystem services (Hooper et al., 2005; McConkey and O'Farrill, 2015).

Seed dispersal is a key process for maintaining ecosystem functionality, consisting of the first stage leading to tree establishment and therefore forest regeneration (Duncan and Chapman, 1999). Among the main advantages of seed dispersal is the removal of seeds away from the parent plant, which increases probability of seed survival and results in colonization of new sites (Traveset and Rodríguez-Pérez, 2019). Indeed, the movement of seeds away from parents plant is pivotal for determining the spatial structure and population dynamics of plants (Nathan and Muller-Landau, 2000). Vertebrates are the main agents responsible for carrying out this process in tropical forests, where about 90% of woody plant species rely on vertebrates to disperse their seeds (Jordano, 2000). In particular, medium and large-sized mammals are key actors for this process, as they play roles that small dispersers cannot perform, such as dispersing large number of seeds, including large seeds and over long distances (Galetti et al., 2001; Bueno et al., 2013).

Plant species bearing large seeds are especially dependent on medium and large-sized mammals to be dispersed. For instance, several tropical trees such as *Joannesia princeps* can only germinate when buried, with the scatter-hoarding agouti (*Dasyprocta leporina*) being the main species able to perform this function (Mittelman et al., 2020).

Furthermore, agoutis and other larger mammals such as tapirs (*Tapirus terrestris*) and primates (e.g., *Brachyteles* spp.) tend to disperse seeds with higher biomass (Bueno et al., 2013; Mittelman et al., 2021). This tight association among large-sized mammals and large seeds in tropical forests ensure that high levels of biomass are kept above ground, thereby maintaining ecosystem services such as carbon storage (Bello et al., 2015, Culot et al., 2017).

On the other hand, several factors can act directly and indirectly to limit seed dispersal, compromising the process effectiveness. Both habitat loss and defaunation can significantly affect the persistence and behavior of key dispersers (Trolliet et al., 2017; Jorge et al., 2013), which in turn impact seed dispersal. For example, Jorge et al., (2013) found that only 16% of the remaining Brazilian Atlantic Forest is still environmentally suitable for retaining the muriquis (*Brachyteles spp*.), an important disperser of large seeds, and other seed disperser and predator species such as the tapir (*Tapirus terrestris*) and the white-lipped peccary (*Tayassu peccary*). Furthermore, there is increasing evidence that poaching can also affect seed dispersal (Wright and Duber, 2001; Holbrook and Loiselle, 2009; Peres et al., 2016), of large-seeded plants that are mainly or exclusively dispersed by large vertebrates–the most vulnerable taxa to poaching pressure in tropical regions (Cullen et al., 2001; Peres and Palacios, 2007; Stones et al., 2007). Consequently, the extirpation or population decline of mammalian seed dispersers can result in undispersed seeds remaining on the forest floor for a longer time, increasing the chances of density-dependent mortality close to the parent plant (Comita et al., 2014), with seed predation by invertebrates having a significant contribution in this regard (Wright et al., 2000; Wright and Duber, 2001). Seed mortality caused by insect predation can exceed 50% of lost seeds beneath the mother plant in defaunated areas (Galetti et al., 2006). Thus, the long-term persistence of plant populations and the ecosystem services provided by them are directly related to the maintenance of the plant-mammal seed dispersal system.

Here, we used structural equation models to assess the direct and indirect effects of spatial predictors and the abundance of potential mammal dispersers on the seed fate of *Eschweilera ovata* in 18 Atlantic Forest fragments in southern Bahia, Brazil. Our conceptual models, summarized in Fig. 1, take into consideration: (i) the direct effect of habitat amount (i.e., patch size and forest cover in the landscape) on seed removal; the indirect effects of (ii) habitat amount; (iii) landscape configuration (i.e., edge density and number of patches); and (iv) anthropogenic stressors (i.e., road density and human population density) via mammal abundance, on the percentage of seeds removed, intact seeds and seeds predated by invertebrates. Specifically, we predicted that seed removal would be lower in larger forest patches and embedded in landscapes with greater habitat amount given the reduced probability of mammals in finding the seeds and the effect of resource dilution (Fig. 1a). Given that mammals negatively respond to both habitat disturbances (Laurance et al., 2009; Fahrig and Rytwinski, 2009; Magioli et al., 2021) and anthropogenic stressors via poaching pressure (Wright, 2003; Franzen, 2006), we predicted that a reduced percentage of seeds will be removed at forest fragments inserted in highly fragmented landscapes dominated by high density of edge, road density and human population (Fig. 1b and 1c). In contrast, we predicted a negative effect of mammal abundance on the percentage of intact and invertebrate preyed seeds, with more seeds remaining intact or preyed by invertebrates in forest fragments presenting low abundance of medium and large-sized mammals (Fig. 1d, 1e and 1f).

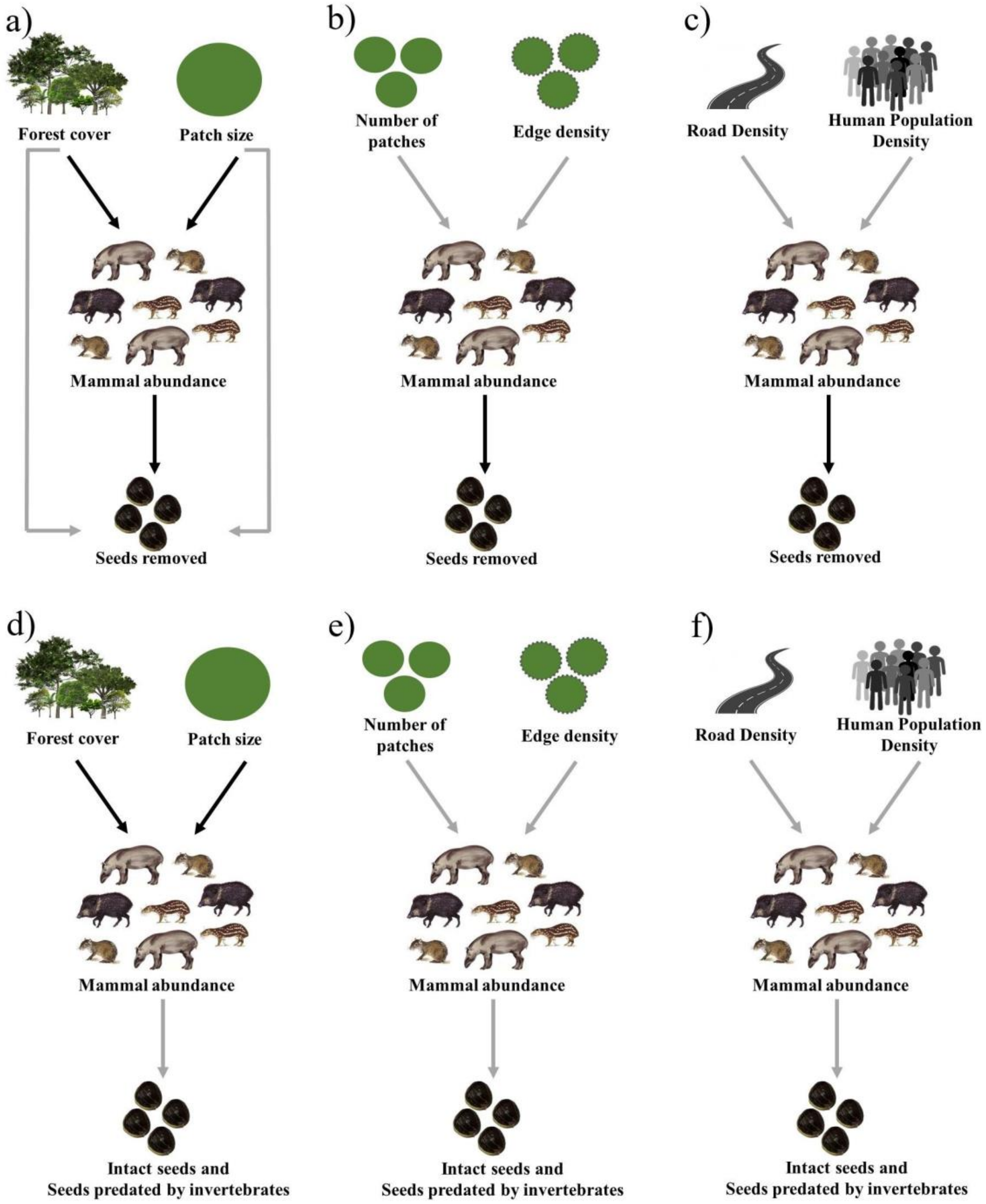

Fig. 1. Theoretical models used to test the direct and indirect effects of spatial predictors and mammal abundance on the percentage of seeds removed (a, b and c), intact seeds and seeds predated by invertebrates (d, e and f). The effects of predictors associated to habitat amount (i.e., patch size and forest cover in the landscape), landscape configuration (i.e., edge density and number of patches) and anthropogenic stressors (i.e., road density and

human population density) are indicated in different models to show potential positive (black arrows) and negative (gray arrows) pathways among variables.

2. Materials and methods

2.1. Study area

This study was performed in 18 Atlantic Forest fragments located in the southern region of the state of Bahia, Brazil (Fig. 2), consisting of 14 private/unprotected areas and four protected areas. Each private area was previously selected by researchers from the REDE SISBIOTA, a research project that evaluates how habitat loss affects biodiversity patterns and processes in anthropogenic landscapes of southern Bahia (see Morante-Filho et al., 2015; Soares et al., 2015 for further details). Protected areas included the Una Biological Reserve, and three National Parks (Pau Brasil, Monte Pascoal and Descobrimento). All comprised large tracts of forest remnants of the Atlantic Forest in Northeast Brazil, being pivotal to safeguard mammal biodiversity in this region (Magioli et al., 2021). The southern Bahia is a megadiverse region with high levels of endemism, but that has a long history of deforestation and degradation of natural forests, mainly through logging and poaching (Canale et al., 2012; Faria et al., 2021). The predominant phytophysiognomy in the region is dense ombrophilous forests (Peixoto et al., 2008), the climate is hot and humid without a dry season according to Köppen classification, and with a mean annual temperature of 24°C and mean annual rainfall of 2,000 mm/year, respectively (Thomas et al., 1998). All forest fragments are inserted within anthropogenic landscapes mainly dominated by cattle pasture, eucalyptus, cacao agroforests and coffee plantations (Magioli et al., 2021).

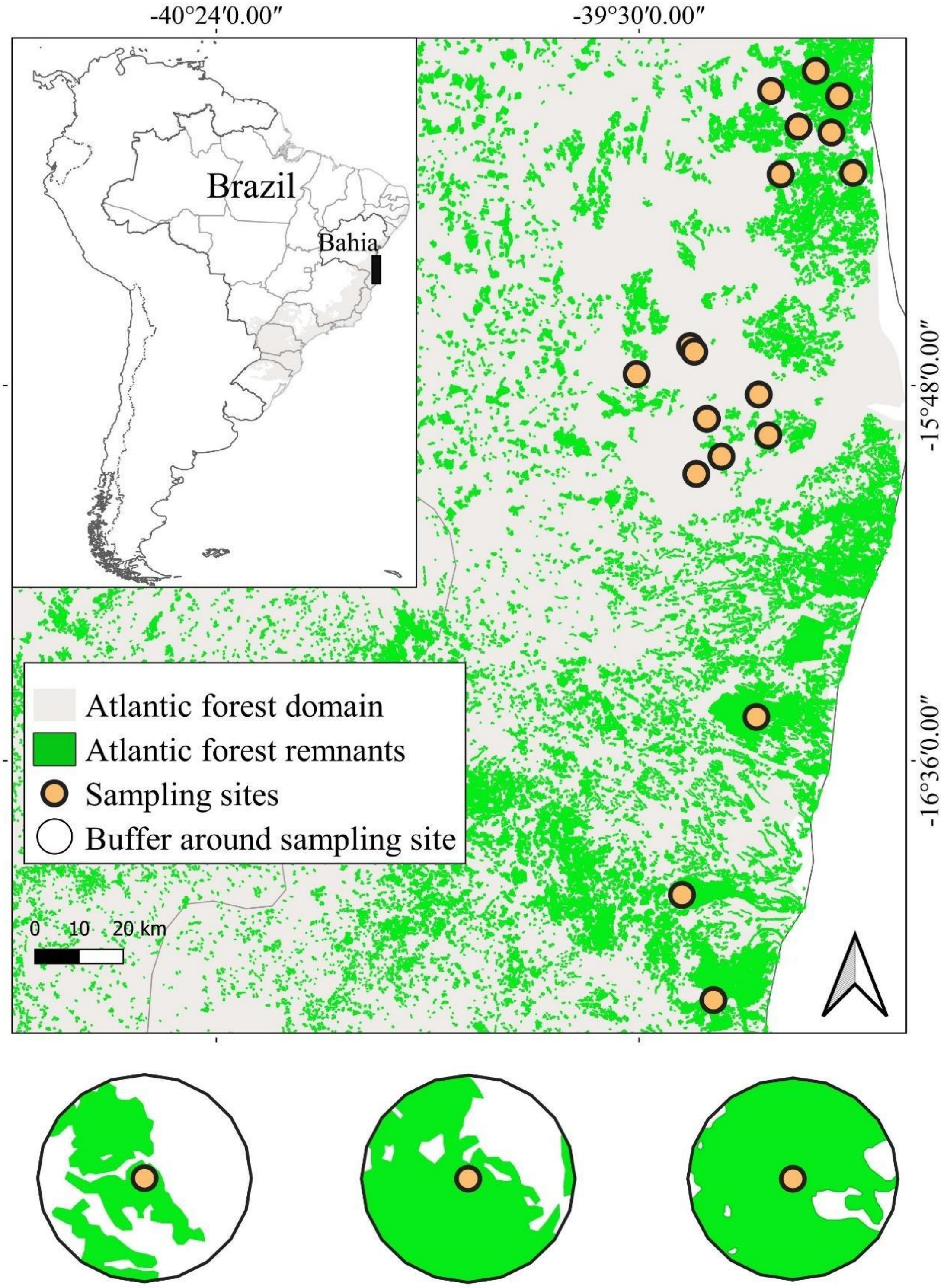

Fig. 2. Location of the 18 Atlantic Forest fragments in the southern region of Bahia, Brazil. At the bottom, we provide examples of three 2 km radius landscapes around the sampling forest fragment, showing differences in landscape habitat amount and configuration.

2.2. Seed dispersal experiment

We set up field experiments to evaluate the seed fate of a large-seeded tree species, *Eschweilera ovata* (Cambess.) Mart. Ex Miers (Lecythidaceae), locally known as biriba. This species is an endemic large tree characteristic of Brazilian old-growth forests, which occurs across the northern portion of the Atlantic Forest (i.e., from Espírito Santo to Pernambuco states), in addition to the western Amazon (Smith et al., 2015). This species is common and widely distributed in the study region, and its fruits comprise a potential source of resource for fauna. Fruits are dehiscent and the dry capsule (30.63 mm diameter/ 21.49 mm length) contains 1 to 4 seeds (17.78 mm diameter/ 20.7 mm length) (Oliveira et al., 2012; Bello et al., 2017). The seeds have a yellow funicular aril that attracts various animals. Although information about the dispersers of *E. ovata* seeds is limited (Vilela et al., 2012), the species depends on medium and large-sized vertebrates for a successful dispersal of its large seeds, with synzoochory being one of the main forms of dispersal (Kimmel et al., 2010).

We established four to 12 experimental stations per forest fragment, depending on the extent of the studied fragment, with a minimum distance of 50 m between stations. Each station consisted of one open treatment containing five threaded seeds of *E. ovata* attached spool to trees at a height of about 35 cm from the ground (adaptation of the spool and line method according to Iob and Vieira, 2008). All seeds were collected in areas proximity or within the surveyed forest fragments. The experiment was performed twice on each fragment, from May to August 2018 (first campaign) and from March to June 2019 (second campaign). Seeds remained for 30 consecutive days in each campaign and after this period, we went back and evaluated the seed fate by including them into four categories: (i) seeds removed – whenever the seed was removed from its initial position, including the seeds that disappeared and the seeds that were found; (ii) intact seeds – when no sign of animal predation was observed or the seeds had germinated; (iii) seeds predated by vertebrates and (iv) seeds predated by invertebrates - as identified based on the signs left on the seeds. For subsequent analyses, we only used information from the three most recorded categories – seeds removed, intact seeds and seeds predated by invertebrates, given that only 2% of total seeds had been predated by vertebrates considering all forest fragments. Also, we used the percentage of seeds in each category (i.e., (the number of seeds included in each category/total number of seeds)*100).

2.3. Mammal surveys

In each forest fragment, we deployed digital camera traps (Bushnell Trophy Cam HD, model 119876) to record medium and large-sized mammal species (> 1 kg, see Paglia et al., 2012; Emmons and Feer, 1997) that are potential dispersers of *E. ovata* seeds. For this, we deployed 1-30 camera traps per forest fragment, without using baits, with the exact number depending on fragment size. The minimum distance between the cameras was 100 meters. Surveys were conducted during three different periods over 2018 to 2020. In 2018 and 2019, surveys at the Pau Brasil National Park were conducted during 60 consecutive days each year. The other fragments were sampled throughout 2019-2020, with varying sampling efforts among sites (minimum of 30 days and maximum of 213 days). This difference between the number of sampling days was due to the COVID-19 pandemic in 2020, which precluded field expeditions to occur and therefore culminated in greater sampling effort in some areas. Camera traps were attached to trees at about 30-40 cm from the ground and operated 24 hrs per day. The sampling effort ranged between

86 and 4238 cameras/day (mean = 567.16, SD ± 968.89) per forest fragments, totaling a sampling effort of 10,209 cameras/day.

We considered *E. ovata* seed dispersers those species with high potential to remove seeds, such as seed scatter-hoarders (e.g., red-rumped agouti - *Dasyprocta leporina*) and other medium and large-sized frugivores such as the paca (*Cuniculus paca*), the lowland tapir (*Tapirus terrestris*) and the collared peccary (*Pecari tajacu*). While it is possible that part of the seeds removed were subsequently predated, we used that seed removal as a proxy of seed dispersal, since the more seeds are removed, the greater the chances of effective dispersal and germination. We also included the small-sized Brazilian squirrel (*Guerlinguetus brasiliensis* – weighing less than 1 kg) in further analyses, because the species was often recorded by camera traps. On the other hand, we excluded disperser species that are mainly associated with consumption of fruit pulp (e.g., deer - *Mazama* sp. and South American coati - *Nasua nasua*. We used capture rates weighted by sampling effort as a proxy of abundance of mammals. For this, we summed the capture rates of each species (individualizing one record every hour) and weighted by the sampling effort of each forest fragment (i.e., total number of records/sampling effort) to estimate the mammal abundance recorded in each forest fragment.

2.4. Spatial predictors

For each sampled fragment, we obtained both patch and landscape metrics. At the patch scale, we delimited the forest patches and estimated their area (PS, in hectares) based on the interpretation of satellite images (Quick Bird and World View from 2011, and Rapid Eye from 2009–2010) using Google Earth Pro. Then, we used the maps of MapBiomas Project – Collection [4, 2019] derived from 30 m resolution Landsat imagery from 2018, downloaded from the Brazilian Annual Land Use and Land Cover Mapping Project (available at < http://mapbiomas. org >) to obtain three landscape metrics: (i) forest cover amount (FC – proportion of native forest, excluding agroforestry), (ii) forest edge density (ED – total perimeter of all forest fragments divided by landscape size) and (iii) number of forest patches (NP – total number of patches within each landscape). In addition, we also collected anthropogenic stressors at the landscape scale, including road density (RD - measured by the total length of roads divided by landscape size) and human population density (HPD - total number of humans divided by landscape size), both extracted from the Instituto Brasileiro de Geografia e Estatística (IBGE) 2010 census. Each landscape variable was calculated using five buffer sizes (i.e., 0.5, 1, 2, 4, 6 km), from the sampling point within each forest fragment. These buffer sizes were chosen according to the available literature on the response of medium and large-sized mammals to landscape changes (see Lyra-Jorge et al., 2010; Beca et al., 2017; Rios et al., 2021). Spatial predictors were calculated in software R v.3.5.2 (R Core Team, 2018) using the package *landscapemetrics* (Hesselbarth et al., 2019) and also using QGIS v.3.4 (QGIS Development Team, 2019).

2.5. Data analysis

We first evaluated the scale of effect (landscape extent) at which the spatial predictors exhibit the greatest influence on each response variable (i.e, seed category - removed, intact, and predated by invertebrates, and the abundance of mammals) (Martin and Fahrig, 2012). For this, we adjusted Generalized Linear Models (GLMs), with negative binomial distribution using the Multifit function (Huais, 2018), which automates the selection process at various spatial scales and relates the response variable to each spatial predictor. We then ranked the models using Akaike Information Criterion (AIC; Burnham and

Anderson, 2004), selecting as the best scale, for each variable, the model that presented the lowest AICc value (Appendix Table A1).

We thus used structural equation models (SEM) to assess direct and indirect effects of spatial predictors and mammal abundance on the percentage of (a) seeds removed, (b) intact seeds, and (c) seeds predated by invertebrates. For this, we first built hypothetical models based on the literature and our knowledge, and considered each spatial variable (i.e., PS, FC, ED, NP, RD and HPD) as exogenous predictors, and the mammal abundance, seeds removed, intact seeds, and seeds predated by invertebrates as endogenous predictors. Since SEM assumes a multivariate normal distribution, we first tested the normality of the data using the Mardia multivariate normality test (Shipley, 2016). Whenever the normality premise was not met, we used logarithmic, arcsine or square root transformations. Given our limited sample size, we defined simple models by using different combinations of variables, and selected those variables that optimized the overall model performance. In particular, our models were composed by two spatial predictors, using only one of the variables related to habitat amount, landscape configuration and anthropogenic stressors at a time in each model (see Fig. 1), in addition to the mammal abundance and one of the categories associated with the seed’s fate. Therefore, each model contained only four variables and 18 observations, totaling 12 models for each category of seed's fate (see Appendix Table A2). Subsequently, we assessed the goodness of fit of each model using the χ^2 test ($P > 0.05$, model with a good fit), Comparative Fit Index (CFI) and Tucker- Lewis Fit Idex (TLI) -CFI and TLI > 0.9, which calculate the relative fit of the observed data compared to the theoretical model. We selected the model with the best fit based on the lowest AIC value, with models presenting a lower than two unities difference in AIC (AIC < 2) were considered parsimonious (see Appendix Table A4). We evaluated the significance of the individual variables of the most parsimonious models using the standardized path coefficients (β) and *P* values ($P<0.05$). We finally assessed the variance of each endogenous variable due to the effect of the other variables using the coefficient of determination (R^2). All statistical analyses were performed in the R 4.0.3 software (R Development Core Team, 2020), using the lavaan package (Rosseel, 2012).

3. Results

Considering all 1,358 deployed seeds across all sampling fragments, a total of 23% exhibited signs of predation – 2% by vertebrates and 21% by invertebrates. In addition, 64% of the overall seeds were removed, 9% remained intact and 4% were infested by fungi. We recorded eight potential seed-dispersal mammal species considering all surveyed fragments: most recorded species included the collared peccary (*Pecari tajacu*; 863 records), paca (*Cuniculus paca*; 371 records) and red-rumped agouti (*Dasyprocta leporina*; 228 records), occurring in 11, 14 and 12 studied forest fragments, respectively (Appendix Table A3).

We obtained a total of one, three, and two parsimonious models (AIC ≤ 2) explaining patterns of seeds removed, intact seeds and seeds predated by invertebrates, respectively (all showing a reasonably good fit; see Appendix Table A4). As the results were similar for all parsimonious models (Appendix Table A5), we present here only the result of the best model. In all examined seed's fate, human population density was negatively and significantly related to the mammal abundance (β = -0.697, Fig 3) (Appendix Table A5). Specifically for seeds removed, we observed a negative effect of forest cover on the percentage of seeds removed (β = -0.587, Fig 3a). Finally, our models were able to explain only a reasonable percentage (34%) of seeds removed and (0.6%) of seed predation by invertebrates (Fig. 3a and c).

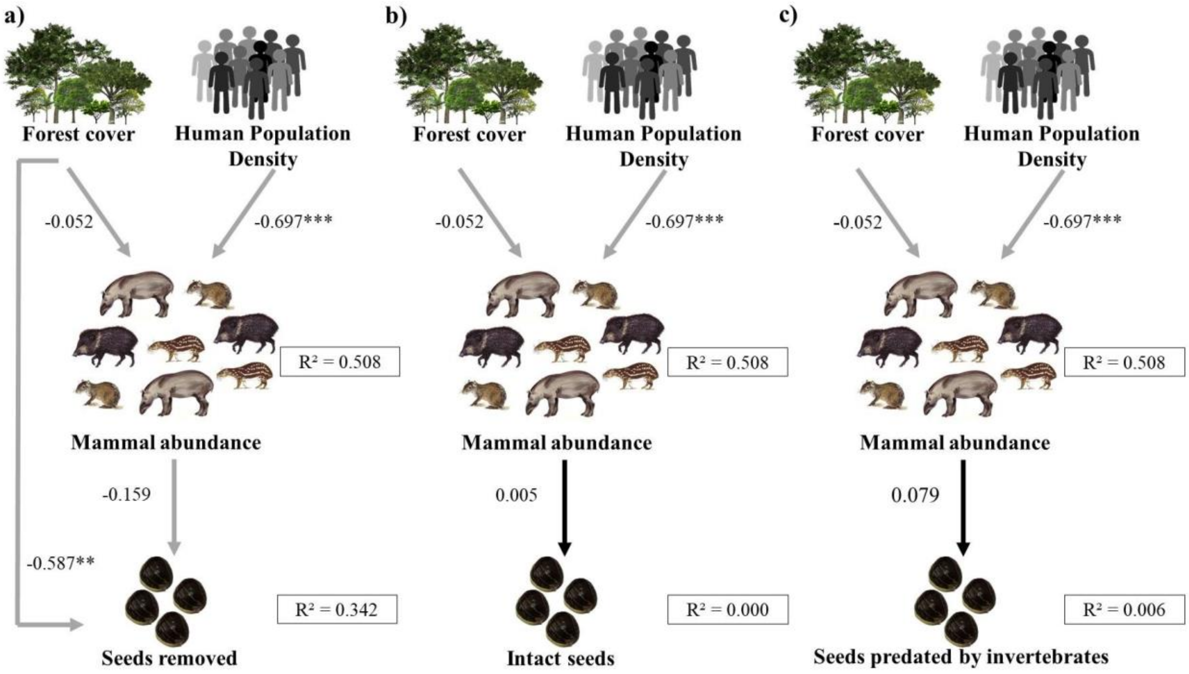

Fig. 3. Best-fitting path model showing the direct and indirect effects of forest cover and human population density on seeds removed (a), intact seeds (b) and seeds predated by invertebrates (c), in 18 Atlantic Forest fragments located in the southern region of Bahia, Brazil. Black and gray arrows represent positive and negative effects, respectively. The significant coefficients are represented by asterisks (**$P < 0.01$ and ***$P < 0.001$) and the coefficient of determination (R^2) of the endogenous variables (mammal abundance, seeds removed, intact seeds and seeds predated by invertebrates) are shown within the rectangles. The results for the other parsimonious models can be observed in Appendix Table A5.

4. Discussion

Our study is the first to assess how the area of the forest fragment and landscape features affect the relative abundance of medium and large-sized mammals and ultimately influence seed removal patterns in anthropogenic Atlantic Forest landscapes. More specifically, our results revealed that the removal of a large-seeded tropical species (*E. ovata*) decreases in more forested landscapes, given that landscape forest amount was a strong direct predictor of seed removal. In addition, the abundance of mammals was drastically reduced in landscapes harboring high human population density, a proxy of anthropogenic stressor potentially related to hunting pressure (Peres and Palacios 2007). These results partially corroborate our hypotheses, and therefore indicate that additional factors could explain overall seed removal patterns in the studied landscapes. We discussed below some mechanisms that might explain the patterns observed in our landscapes.

As predicted, we found a direct negative effect of landscape-scale forest cover on the percentage of *E. ovata* seed removal. Since disturbances reduce habitat quality and negatively affect the availability of food resources (Arroyo-Rodríguez and Mandujano, 2006; Cudney-Valenzuela et al., 2021), seeds available in forest fragments inserted in deforested landscapes may be promptly removed by mammals. Conversely, in more forested landscapes two alternative and non-exclusive scenarios may occur: (i) a lower encounter rate of mammals with the seeds in larger areas, and (ii) a greater fruit availability, resulting in seed-disperser mammals using different strategies to select preferred resources, causing a dilution in dispersal rates between species. In fact, landscape forest loss decreases richness, abundance and fruit biomass of zoochoric tree species in our study region (Pessoa et al., 2016). Thus, high deforested landscapes retain lower resource availability, increasing the chances that mammal would use all available resources, regardless of whether they are their preferred resources. However, it is important to highlight that the high seed removal in deforested landscapes does not necessarily imply that dispersal is successful in these landscapes. While several studies have revealed that habitat loss has negative effects on seedling recruitment, predation and seed dispersal, and loss of disperser species, including other taxonomic groups (Moran and Catterall, 2014; Soares et al., 2015; Trolliet et al., 2015; al., 2017), here we limit our conclusions to a seed removal experiment of *E. ovata* seeds in Atlantic Forest fragments in southern Bahia.

We also found a negative effect of human population density on the abundance of potential mammal dispersers, confirming our hypothesis. In fact, the negative impact caused by human presence on mammals across tropical forests is relatively well known, causing, for example, habitat destruction and increased poaching pressure, which may have synergistic effects (Peres, 2000; Franzen, 2006; Romero-Muñoz et al., 2020). In addition, mammal population declines tend to be more intense near human settlements and in sites where there is greater access to urban centers (Benítez-López et al., 2017). Especially in the Atlantic Forest, which is home to 70% of the Brazilian human population (SOS Mata Atlântica and INPE, 2020), poaching activity took place over the years of colonization of the territory and is currently still widely distributed in the biome (Galetti et al., 2021), including in protected areas (Cullen Jr et al., 2000; 2001; Castilho et al., 2017), with catastrophic effects on the persistence of mammals (Canale et al., 2012). We indeed recorded several instances of poaching evidence in our studied fragments, including photos of hunters and dogs on camera traps, traps and hunting platforms, both inside and outside of protected areas. In addition, there are usually other factors acting simultaneously with poaching in anthropogenic landscapes (such as wildfires, introduction of alien species and infectious disease; Smith et al., 2006; Da Rosa et al., 2017), which can intensify the vulnerability of mammal populations, which, added to certain attributes, such as low reproductive rates, long generation times and large body size slow down the recovery of these populations (Bodmer et al., 1997; Ripple et al., 2016).

Contrary to our expectations, we found no significant effect of the abundance of mammal dispersers on the percentage of seeds removed. These results differ widely from the literature (Galetti et al., 2006; Trolliet et al., 2017; Escobar et al., 2020), suggesting that there may be other factors influencing seed removal in the studied landscapes. For instance, given the high percentage of seeds removed in our study (64%), it is possible that there are limitations in our sampling method for detecting potential dispersers. Here, we restrict our sampling to medium and large-sized terrestrial mammals, given that camera traps are an efficient method to detect this group (Srbek-Araujo and Chiarello, 2005). However, we did not evaluate other biological groups such as small rodents, primates and other arboreal species that may play an important role in removing seeds. In fact, Vilela et al., (2012) recorded primates such as the buff-headed capuchin (*Sapajus xanthosternos*) and the black-handed titi (*Callicebus melanochir*) interacting with *E. ovata* seeds. Alternatively, it is possible that some invertebrates can also manipulate seed and eventually remove them. For example, dung beetles play an important role as a secondary disperser, including being able to disperse seeds similar in size to those of *E. ovata* (Andresen, 2002; Andresen and Feer, 2005).

We also did not detect a significant effect of mammal abundance on the percentage of intact and seeds predated by invertebrates. We expected that the failure of seed dispersal, caused by the low abundance of mammals, would increase the chances of seed germination and decreased seed survival due to invertebrate predation, a pattern found in other forest areas (Wright et al., 2000; Galetti et al., 2006). Although this relationship has not been found, invertebrates preyed on a significant portion of available seeds (21%), contributing to seed mortality. This may have important implications for recruitment (Wright et al., 2001; Dracxler et al., 2011).

5. Conclusion

Habitat changes and the loss of large seed disperser mammals can have important consequences for the functioning of ecosystems, but these relationships are often complex and we are still beginning to understand them. Given the rising rates of deforestation and other anthropogenic pressures on tropical forests (Gibson et al., 2011), understanding the consequences on forest functionality is critical to conservation. Our results show the relevance of forest cover in the landscape for seed removal and demonstrate how intricate these relationships can be. We also showed the influence of human population density on mammal abundance. Here, we highlight that although curbing deforestation is a priority measure for the conservation of various groups of organisms that occur in the Atlantic Forest (Jorge et al., 2013; Morante-Filho et al., 2015; Rocha-Santos et al., 2017), for seed disperser mammals this action is not enough. We therefore recommend that conservation strategies incorporate mitigation measures in landscapes with high human density, as they can act as a drain by drastically reducing the abundance of disperser mammal populations, mainly via poaching pressure (Peres 2000; Cullen Jr. et al., 2001). Among these measures, we suggest that the (i) implementation of environmental education programs be developed in the communities surrounding these forest fragments, aiming to sensitize people about the importance of local fauna and ecosystem services provided by them and (ii) development whether adding value to local products or generating other income alternatives for communities. Furthermore, we recommend that enforcement be strengthened, especially in and around protected areas, and that environmental laws are effectively enforced. These measures are relevant, as although the abundance of mammals did not affect the removal of *E. ovata* seeds in our study, these species are important dispersers of other seeds, including large seeds that contribute to carbon storage in forests (Galetti et al. al., 2001; 2006).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Material

Appendix A: supplementary material of the manuscript: Linking landscape features, anthropogenic stressors and mammal abundance to unveil seed removal patterns in tropical deforested landscapes

Table A1 – Generalized Linear Models showing the selected scale of effect of each response variable (FC = Forest cover, ED = Edge density, NP = Number of patches, RD = Road density and HPD = Human population density). The scale of effect with the lowest AIC value are highlighted in bold.

	FC	ED	NP	RD	HPD
Seeds removed					
0.5 km	177.074	-	-	-	-
1 km	176.994	-	-	-	-
2 km	175.805	-	-	-	-
4 km	**173.866**	-	**-**	**-**	-
6 km	175.484	**-**	-	-	**-**
Mammal abundance					
0.5 km	**19.968**	19.965	20.025	19.934	**19.135**
1 km	20.058	20.063	**20.024**	20.046	19.278
2 km	20.038	20.021	20.072	19.814	19.699
4 km	20.012	**19.822**	20.072	19.858	19.881
6 km	19.985	19.971	20.062	**19.744**	19.964

Table A2. Path models constructed using different combinations of variables which were used in the models with seeds removed (SR), intact seeds (IS) and seeds predated by invertebrate (PI). PS = Patch size, FC = Forest cover, ED = Edge density, NP = Number of patches, RD = Road density, HPD = Human population density and MA = Mammal abundance.

Model	**Variables**
Seeds removed	
1	PS+ED+MA+SR
2	PS+NP+MA+SR
3	PS+RD+MA+SR
4	PS+HPD+MA+SR
5	FC+NP+MA+SR
6	FC+ED+MA+SR
7	FC+HPD+MA+SR
8	FC+RD+MA+SR
9	NP+RD+MA+SR
10	NP+HPD+MA+SR
11	ED+RD+MA+SR
12	ED+HPD+MA+SR
Intact seeds	
1	PS+ED+MA+IS
2	PS+NP+MA+IS
3	PS+RD+MA+IS
4	PS+HPD+MA+IS
5	FC+NP+MA+IS
6	FC+ED+MA+IS
7	FC+HPD+MA+IS

8	FC+RD+MA+IS
9	NP+RD+MA+IS
10	NP+HPD+MA+IS
11	ED+RD+MA+IS
12	ED+HPD+MA+IS
Seeds predated by invertebrates	
1	PS+ED+MA+PI
2	PS+NP+MA+PI
3	PS+RD+MA+PI
4	PS+HPD+MA+PI
5	FC+NP+MA+PI
6	FC+ED+MA+PI
7	FC+HPD+MA+PI
8	FC+RD+MA+PI
9	NP+RD+MA+PI
10	NP+HPD+MA+PI
11	ED+RD+MA+PI
12	ED+HPD+MA+PI

Table A3 – Mammal species recorded with camera traps considering all 18 Atlantic Forest fragments in southern Bahia, Brazil, including the number of forest fragments in which each species was recorded.

Species	**Common name**	**Number of forest fragments**
Rodentia		
Cuniculidae		
Cuniculus paca (Linnaeus, 1766)	Agouti	14
Dasyproctidae		
Dasyprocta leporina (Linnaeus, 1758)	Red-rumped Agouti	12
Sciuridae		
Guerlinguetus brasiliensis	Squirrel	12
Didelphimorphia		
Didelphidae		
Didelphis aurita (Wied-Neuwied, 1826)	Southeastern Common Opossum	16
Didelphis albiventris (Lund, 1840)	White-eared Opossum	2
Cetartiodactyla		
Tayassuidae		
Pecari tajacu (Linnaeus, 1758)	Collared Peccary	11
Tayassu pecari (Link, 1795)	White-lipped Peccary	1
Perissodactyla		

Tapiridae		2
Tapirus terrestris (Linnaeus, 1758)	Tapir	

Table A4 - Models' fit coefficients for seeds removed (SR), intact seeds (IS) and seeds predated by invertebrates (PI). Where, PS = Patch size, FC = Forest cover, ED = Edge density, NP = Number of patches, RD = Road density, HPD = Humana population density, and MA = Mammal abundance. The most parsimonious models are highlighted in bold (see details of the best models in Table A5).

Model	χ^2	**CFI**	**TLI**	**AIC**
Seeds removed				
FC+HPD+ MA+SR	**0.540**	**1.000**	**1.091**	**146.082**
PS+HPD+ MA+SR	0.585	1.000	1.086	148.268
ED+HPD+ MA+SR	0.002	0.647	0.118	149.208
NP+HPD+ MA+SR	0.182	0.916	0.789	151.583
FC+ED+ MA+SR	0.059	0.704	0.310	151.762
FC+RD+ MA+SR	0.587	1.000	1.074	152.560
PS+RD+ MA+SR	0.519	1.000	1.048	155.117
ED+RD+ MA+SR	0.001	0.751	0.378	156.295
FC+NP+ MA+SR	0.501	1.000	1.314	156.984
PS+ED+MA+SR	0.005	0.409	-1.957	157.663
NP+RD+ MA+SR	0.184	0.952	0.879	158.376
PS+NP+ MA+SR	0.474	1.000	1.948	159.296
Intact seeds				
FC+HPD+MA+IS	**0.671**	**1.000**	**1.351**	**57.149**
NP+HPD+MA+IS	**0.591**	**1.000**	**1.271**	**57.233**
PS+HPD+MA+IS	**0.408**	**1.000**	**1.014**	**57.241**
ED+HPD+MA+IS	0.006	0.621	0.054	54.858
ED+RD+MA+IS	0.008	0.718	0.296	61.944
FC+ED+MA+IS	0.005	0.321	-0.697	62.829
FC+RD+MA+IS	0.712	1.000	2.672	63.627
NP+RD+MA+IS	0.643	1.000	2.569	64.025

PS+RD+MA+IS	0.399	1.000	1.007	64.090
PS+ED+MA+IS	0.007	0.035	-1.412	66.636
FC+NP+MA+IS	0.631	1.000	-0.222	68.051
PS+NP+MA+IS	0.401	1.000	0.718	68.269
Seeds predated by invertebrates				
ED+HPD+MA+PI	0.002	0.572	-0.069	34.934
FC+HPD+MA+PI	**0.293**	**0.956**	**0.890**	**37.226**
NP+HPD+MA+PI	**0.375**	**1.000**	**1.009**	**37.310**
PS+HPD+MA+PI	0.032	0.882	0.704	37.317
ED+RD+MA+PI	0.004	0.680	0.200	42.021
FC+ED+MA+PI	0.004	0.311	-0.721	42.905
FC+RD+MA+PI	0.465	1.000	1.398	43.704
NP+RD+MA+PI	0.578	1.000	2.074	44.102
PS+RD+MA+PI	0.088	0.952	0.879	44.166
PS+ED+MA+PI	0.004	0.041	-1.397	46.713
FC+NP+MA+PI	0.428	1.000	0.424	48.127
PS+NP+MA+PI	0.100	0.000	-3.756	48.345

Table A5. Best-fitted path models showing the direct and indirect effects of spatial variables (patch size, number of patches and human population density) on intact seeds and seeds predated by invertebrates, in 18 Atlantic Forest fragments located in the southern region of Bahia, Brazil. The significant paths are highlighted in bold.

Model	**Estimate**	**Standard error**	**Z-value**	***P*-value**	**Std.all**
Seeds removed					
Mammal abundance ~					
Forest cover	-0.030	0.099	-0.303	0.762	-0.052
Human population density	**-5.871**	**1.448**	**-4.054**	**0.000**	**-0.697**
Seeds removed ~					
Forest cover	-59.040	19.442	-3.037	0.002	-0.587
Mammal abundance	-25.582	31.129	-0.822	0.411	-0.159
Intact seeds					
Mammal abundance ~					
Forest cover	-0.030	0.099	-0.303	0.762	-0.052
Human population density	**-5.871**	**1.448**	**-4.054**	**0.000**	**-0.697**
Intact seed ~					
Mammal abundance	0.063	2.753	0.023	0.982	0.005
Mammal abundance ~					
Number of patches	-0.003	0.032	-0.088	0.930	-0.015
Human population density	**-6.024**	**1.445**	**-4.169**	**0.000**	**-0.715**
Intact seed ~					
Mammal abundance	0.063	2.753	0.023	0.982	0.005
Mammal abundance ~					
Patch size	-0.000	0.000	-0.005	0.996	-0.001
Human population density	**-5.992**	**1.413**	**-4.242**	**0.000**	**-0.711**

Intact seed ~					
Mammal abundance	0.063	2.753	0.023	0.982	0.005
Seeds predated by invertebrates					
Mammal abundance ~					
Forest cover	-0.030	0.099	-0.303	0.762	-0.052
Human population density	**-5.871**	**1.448**	**-4.054**	**0.000**	**-0.697**
Intact seed ~					
Mammal abundance	0.531	1.583	0.335	0.737	0.079
Mammal abundance ~					
Number of patches	-0.003	0.032	-0.088	0.930	-0.015
Human population density	**-6.024**	**1.445**	**-4.169**	**0.000**	**-0.715**
Intact seed ~					
Mammal abundance	0.531	1.583	0.335	0.737	0.079

CONCLUSÃO GERAL

De maneira geral, os resultados aqui obtidos elucidam sobre os principais determinantes da riqueza e ocorrência dos mamíferos de médio e grande porte em paisagens florestais modificadas pelo homem ao longo da Mata Atlântica brasileira, além de identificar quais os efeitos diretos e indiretos de características espaciais em escala de mancha e de paisagem sobre potenciais dispersores e o processo de remoção de sementes. Mais especificamente, a partir dos resultados encontrados no primeiro capítulo, onde a riqueza de mamíferos aumentou com a quantidade de habitat na paisagem, nós demonstramos a importância de manter fragmentos florestais imersos em paisagens altamente florestadas para garantir uma alta riqueza de mamíferos. Além disso, revelamos que a fragmentação *per se* tem efeitos consistentemente fracos, com exceção para riqueza de herbívoros que declinou em paisagens com maior número de manchas. Conter o avanço do desmatamento na Mata Atlântica e fomentar projetos de restauração florestal devem ser medidas prioritárias para salvaguardar uma alta riqueza de mamíferos de médio e grande porte. Além disso, manter esses fragmentos florestais imersos em uma matriz mais amigável pode ser uma estratégia importante para manter a alta riqueza de herbívoros.

No segundo capítulo, revelamos que, em sua a maioria, os fragmentos florestais da Mata Atlântica estão esgotados de várias espécies de mamíferos terrestres de médio e grande porte, com apenas dois fragmentos florestais estudados retendo >80% das espécies esperadas. Enquanto o padrão geral de ocorrência das espécies foi determinado pelo tamanho da mancha, distúrbios antrópicos e massa corporal das espécies, as respostas individuais das espécies variaram amplamente. Algumas delas correm sérios riscos de desaparecer devido à sua alta sensibilidade às mudanças na paisagem, enquanto outras espécies podem se adaptar e persistir nessas mesmas paisagens. De maneira geral, para garantir a ocorrência das espécies de mamíferos terrestres nas paisagens da Mata Atlântica, é importante manter grandes fragmentos florestais na paisagem e mitigar principalmente os efeitos de borda e das estradas.

No terceiro capítulo, demostramos que a cobertura florestal foi o único preditor capaz de explicar a remoção de sementes de *E. ovata*. Sugerimos que a baixa remoção de sementes em paisagens altamente florestadas pode ser explicada pela menor probabilidade dos mamíferos encontrarem as sementes (efeito de diluição) ou a menor probabilidade dos mamíferos consumirem essas sementes devido à alta disponibilidade de recursos. Também revelamos que é importante manter uma baixa densidade populacional humana na paisagem para assegurar uma alta abundância de mamíferos dispersores, incluindo as cutias e as antas. Dado que a presença humana é um *proxy* de atividades antrópicas como a caça, recomendamos que ações de fiscalização sejam intensificadas nos fragmentos florestais, visando coibir a prática da caça que é histórica e amplamente difundida no bioma (CANALE *et al*. 2012). Nós também sugerimos o desenvolvimento de programas de Educação Ambiental, principalmente em áreas no entorno dos fragmentos florestais, que promovam práticas que busquem minimizar os impactos das atividades humanas, como a caça, sobre os mamíferos. Finalmente, os resultados apresentados aqui revelam que conter o avanço do desmatamento é uma ação prioritária, mas não é suficiente para conservar os mamíferos de médio e grande porte e a provisão dos serviços ecossistêmicos. Nós também recomendamos fortemente a restauração florestal em larga escala, o desenvolvimento de programas de Educação Ambiental e o fortalecimento das políticas ambientais. Além disso, visto a severa defaunação dos quais os fragmentos estudados se encontram atualmente, os esforços não podem ser limitados a medidas de manejo exclusivamente relacionadas com a paisagem. A reintrodução de espécies-chave, como antas, cutias e outros mamíferos, que já foram extintos localmente em diversos fragmentos, é recomendado para restabelecer as populações e interações ecológicas (CID *et al*. 2014; FERNANDEZ *et al*. 2017).

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